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THE SOCIAL ASPECTS OF POPULATION DYNAMICS

BY JOHN B. CALHOUN

The subject of population dynamics is more commonly treated from the demographic point of view. This view stresses the fact that a population grows, remains stable, or declines, dependent upon the interrelationships of natality, mortality, and migration. Interactions of these phenomena determine density; that is, the number of organisms inhabiting a given space. Customarily, the results of such demographic studies are graphed as growth curves which pictorially show the change in density through time, or they are given as life tables from which such factors as life expectancy or age structure of the population may be derived.

In the analysis of those factors which alter the pattern of changes in density, consideration is normally given to the relative abundance of food or other prerequisites of life, to the incidence of disease and similar factors as they affect the general health of the population, and to the occurrence of favorable or unfavorable climatic conditions. Such factors are viewed as they depress or accelerate the growth and expansion of a population (Allee, *et al.*, 1949; Cole, 1948; Park, 1946). Scant attention is paid to the role of the individual or to the internal phenomena of those sub-groups of the population to which every individual of most species is normally a member, such as the family or other reproductive aggregates, feeding aggregations, harborage aggregations, and finally regional aggregations. This latter consists of individuals or groups which occasionally come in contact with each other without normally participating in the attaining of common goals. "If social behavior really does alter the character of population dynamics, it is just such an understanding of the role of the individual and his group which we must seek." We might have rephrased our problem as "Does population dynamics alter the character of social behavior?" Both aspects will be examined here.

In the following discussion there is no attempt to review the literature. Rather, we shall hazard to discuss a wide variety of phenomena that are involved in a full appreciation of the interrelationship between sociality and population dynamics. Through such a "stock-taking" of relevant data from diverse fields of research, we shall endeavor to demonstrate the need for multi-discipline approaches to these complex problems. The writer, as an ecologist, no doubt expresses bias in his treatment of this discussion.

We might first wonder if sociality really does have any influence at all on population dynamics. Perhaps it will be best for me to describe briefly a situation with which I have had intimate experience. This concerns the role of social

behavior in limiting numbers among wild Norway rats. (This study of the Norway rat is still largely unpublished. It was a phase of the research program of the Rodent Ecology Project of the Johns Hopkins University School of Hygiene and Public Health, which was sponsored through a grant from the International Health Division of the Rockefeller Foundation.) (Calhoun, 1949*a*, 1949*b*.) For 28 months I observed a colony of rats (*Rattus norvegicus*) near Towson, Maryland, as it grew from a few individuals to the point of saturation in numbers. This colony was maintained in a 10,000-square-foot pen where there was a superabundance of food at all times, and where harborage space was never completely utilized by the rats. At the time the colony was killed off there were considerably less than 200 adult rats, and all the evidence pointed to the fact that the adult population would never have exceeded 200 individuals. The number is particularly instructive when we compare it with the number of rats that might have been raised in the available space had each individual been isolated as a juvenile into two square feet of cage space, as is customarily done in the laboratory. Under such laboratory conditions 5,000 healthy rats might have been reared in 10,000 square feet of space instead of the 200 which utilized such space under free ranging conditions. This figure of 5,000 rats is actually a conservative one in regard to representing the biotic potential expected from this free-ranging colony. The studies of Emlen and Davis (1948) and Davis (1949) supplemented by my own observations indicate the following conditions for determining the potential reproduction were other limiting factors not in operation: (1) 8 per weaned litter with equal sex ratio; (2) first litter by 5 months of age; (3) one litter every two months; (4) no breeding during the four mid-winter months; (5) all rats born the first breeding season should be dead by the end of the third; (6) it is within the potential life span of a rat for all others to have been alive at the end of the experiment; (7) the study lasted from March 1947 to June 1949. With these conditions as a basis for judgment, 50,000 rats might have been alive in June 1949 as descendants from the original five females. Nevertheless, in the comparison above, it is believed that the figure 5,000 is a more realistic one in indicating the potential density of 10,000 square feet, although it is conceivable that 50,000 healthy rats could be maintained in a similar space by confining each to a cage somewhat less than eight inches on a side. What, then, was the cause of this 25-fold decrease in utilization of space under naturalistic conditions? The obvious explanation is that under free ranging conditions the rats expressed genetically determined and culturally modified behavioristic potentialities, which were impossible under caged conditions. This explanation has philosophically broad implications. Whenever the density of a population becomes increased beyond that level to which the heredity-to-environment relationship provides optimum adjustment, then the individual and the group must forfeit some of their potentials of behavior if all members are to maintain an adequate state of health.

There are three basic ways in which the social behavior of this colony of rats altered the population growth. They are as follows:

1. *Development of local groups which maintain their integrity restricts the utilization of space.*—Local colonies or aggregates were formed primarily on the basis of continued association in the locality of birth. There was sufficient conflict existing between these local colonies that there developed intermediate buffer zones in which burrows were never constructed and across which there was a reduced incidence of locomotion. The development of these social buffer zones seems essential to the maintenance of group integrity and it is a major factor in reducing the number of animals which utilize a given amount of space.

2. *Social stability favors successful reproduction.*—A stable group is one in which there is a well-developed dominance hierarchy, is one where there are well-established relationships between all the members of the group, and is one in which the individual members have experienced few behavioral disturbances and have exhibited favorable patterns of growth. Among such stable groups the frequency of conception is high, and most of the young born are successfully raised.

On the contrary, among socially unstable groups the frequency of conception is reduced and very few of the young born survive to weaning, and if they do the chances of their, in turn, leaving any progeny are very slim indeed. Socially unstable groups are those consisting of members who have had few associations in common, and/or who have experienced many behavioral disturbances and have exhibited retarded rates of growth. Such groups normally have an unstable or poorly defined hierarchial system.

3. *Social stability favors decreased mortality.*—Predation from flies was the chief direct cause of death. During the immediate post-weaning period, when the young rats are making their adjustments to colony life, flies frequently lay eggs in the fur of the young. The young most likely to succumb are those which have received excessive punitive action from their associates or who, for various reasons, have no permanent home. Flies also kill adults by laying eggs in open wounds, even fresh wounds. Rats low in the social order receive more wounds and are thus more subject to being consumed "alive" by maggots.

As the population increased in numbers there was an increase in the frequency, intensity, and complexity of behavioral adjustments necessitated among and between groups of rats. This forced more and more rats to be characterized by social instability with the accompanying result of lowering the biotic potential to the point where there was a balance between natality and mortality—all this in the continued presence of a superabundance of food and unused space available for harborage.

This influence of social behavior upon population growth in the Norway rat is exhibited in various degrees among other animals. However, in the time and space available here, no attempt will be made to present a critical review of the field. Rather, we shall examine the phenomena of social behavior and the condition of sociality as they relate to the broad problem of growth exhibited both on the individual and on the population level. Through this discussion we

shall place sociality in perspective to other biological phenomena and suggest avenues for further research.

Various concepts of levels or types of sociality exist. According to Allee (1940) these are: 1. "Sociality includes all integrations of two or more organisms into a supra-individualistic unity on which natural selection can act;" 2. Sociality is coextensive "with the existence of an innate pattern of a certain specialized appetite" whose satisfaction demands that animals live together and engage in common activities; 3. "True sociality occurs only in the presence of abstract values of which members of the group are more or less conscious." Thus, sociality ranges from unconscious automatic co-operation (Allee, 1945) to conscious co-operation in which the members react to socially conditioned symbols (Northrop, 1948). A bridging of this range of social characteristics is begun as soon as the association between a social behavior and its consequences is modified by the learning process. For example, when a mouse who has repeatedly lost in combat makes the adjustment of running away upon sight of his opponent, values are affecting social behavior. Approaching the opponent will result in pain, while avoidance prevents pain. Not only does such a behavior illustrate the realization of values, but also that such values may be generalized. A case (Allee, 1942) in point is that of an albino mouse, who submits to other albino mice on first encounter, after having previously been conditioned from repeated defeats by the more aggressive C57 black mice. To such a mouse any other mouse, and not just the one by which it had been beaten, serves as a symbol of the dire consequences which will result, if he fails to submit or run away. Such generalizations from prior experience form the major basis for the origin of abstract values.

For our consideration of the interrelationship of sociality to growth phenomena, the most important considerations cover those conditions permitting a population to develop and express those characteristics of sociality which are possible within the limitations imposed by the genetic potentialities of the species in question.

Wherever animals live they are constantly altering the environment about them. This occurs through such diverse phenomena as release of excreta, alteration of surrounding temperature and humidity, construction of trails and burrows, and the development of habits, all of which may alter the behavior of members of their own or later generations. These phenomena are spoken of as biological conditioning of the environment. Such activity has repeatedly been shown to alter the welfare of existing members of a population as well as the density exhibited by later generations (Allee, 1942, 1945; Allee, *et al.*, 1949). Under essentially random dispersal of individuals through the environment, any effect of biological conditioning upon the welfare of the members of a population may be assumed to be dissociated from social phenomena. However, when such effects are associated with animals which live in aggregates (as opposed to different effects occurring when the same kind of animals live dispersed) we may, with assurance, infer that sociality is a factor in affecting the welfare of the group. There is a tendency among many animals toward group activity, the result of which ameliorates the environment so that their physiology is more efficient or that survival rate is increased. Such biologically conditioning phe-

nomena are the result of co-operative activity. Beyond a certain point the same activity may become deleterious as the participating group increases in numbers, to the point that the formerly beneficial activity lowers survival rate or physiological efficiency. *The merits of any social behavior are thus relative to the condition and history of the group within which they occur.* For example, copulation among mammals is a desirable and necessary social behavior if the species is to survive. Yet, among certain socially disturbed groups of my Towson colony of rats, which lacked a well-integrated dominance-hierarchy, copulation rarely led to conception despite, or perhaps because of, its high frequency.

As soon as animals begin to condition their environment through the elaboration of relatively permanent artifacts such as trails, nests, burrows, and the like, biological conditioning assumes a more definite cultural aspect. To be sure, such artifacts satisfy primary organic requirements; dens are a place of retreat from enemies or inclement weather; nests are places where the young are safe; trails lead to food or harborage, and food caches serve to make food more accessible. However, beyond such primary functions, dens, nests, trails and the like further serve as a physical mold in which the social matrix takes its form.

It is with reference to the construction and utilization of these animal-made structures that many patterns of behavioral relationships become established. Where more than one animal uses one of these biological artifacts either conflict, tolerance, or the acceptance of rank-oriented priority develops (Collias, 1944). When two rats, who are familiar with each other, meet along a trail, each usually steps slightly aside and passage occurs with no sign of conflict, even where difference in rank occurs. Furthermore, young animals who develop within an artifact-conditioned environment find life much easier than did the original colonizers. They not only find previously established places of retreat and established pathways of movement between harborages, sources of food and the like, but they also encounter an artifact-oriented stabilized social structure within which their own integration during maturation is facilitated.

This alteration of the habits and social behavior of one generation by the activities of generations which precede it represents a cultural process, when culture is considered from a broad biological viewpoint. The term culture will here be used in this limited sense, without attempting to discuss the further elaborations which are expressed among human societies. If this restriction is placed upon the concept of culture, there exists the possibility of treating it comparatively in experiments with infra-human organisms. By so doing we may hope to arrive at generalizations which are useful on the human level. For such comparative purposes we can deal with effects and modifications produced by inherent behavior as well as those which are further structured through the process of learning.

There are striking similarities between the culture of man and that of some of the other vertebrates. Artifacts are constructed, learned patterns of social behavior are developed, and both are passed on to influence the life of later generations. Chance behavior or superstition may affect the pattern of learned social behavior (Skinner, 1948), and the character of vocalization may be handed down through cultural inheritance. Regarding the cultural modification of vocali-

zation, Altmann (1950) has recently described an interesting situation among elk. In herds whose social structure has been upset by hunting, very little vocalization occurs. However, in a herd which lived far back in the Teton Mountains, where they had escaped being hunted, there was a continual calling back and forth between members of the herd.

Much in common exists between the patterns of culture among different species of vertebrates. Culture, particularly when continuity through many generations is insured, provides a stabilizing influence on the activities of the members of a population and permits them to make more effective use of their environment. Although there is as yet no experimental data to verify this postulate, it is quite likely that the genetic inheritance of many species is such that optimum adjustment by the individual or the group is made only under those conditions favoring the existence of a stabilized culture with its accompanying biologically produced artifacts. However, we must realize that cultural stability also restricts the potentialities of behavior, since other patterns of culture are automatically excluded.

It is through the alteration of the complexity and stability of culture that sociality exerts a controlling influence upon population dynamics. One of the inherent aspects of this concept concerns the relative continuity through space and time of both the population and the physical and social alterations which have been produced by the population. Discontinuities impose conditions of cultural instability as well as inhibit the maintenance of developing complexities of social organization. As mentioned previously, for the Norway rat such social control of population dynamics operates by influencing reproductive capacity, growth rate, mortality rate, incidence of disease, and behavioral adjustment. Our problem, then, resolves itself into a consideration of factors which may influence the complexity or stability of the culture of a population.

Analysis of operant factors must take into consideration the perception of the environment by the individual. The manner in which animals perceive their environment is socially important because it largely determines the rate and manner in which animals contact each other, and the manner in which they utilize the space about them. We often overlook the fact that the same physical environment, such as a mat of grass, may be differently perceived or is differently reacted to by different organisms (Schneirla 1949). Similarly, the same environment may have different meaning to two different individuals of the same species, due to differences in heredity or experience. In this discussion we shall treat the responses (or lack of responses) of animals as resulting from their perception of the environment. However, we must realize that the physiological state of the individual may alter the response regardless of how the environment is perceived (Fuller, 1950).

There are two phenomena relative to perception of the environment which must be kept in mind upon interpreting observations. First, an animal may react to an environmental situation as if it were complete, whereas portions of it are actually missing. Second, an animal may fail to perceive or react to portions of its environment which are actually present, and which it is capable of

perceiving and reacting to. In either case, unfavorable usage of the environment, with resultant density effects, may occur.

The first phenomenon of reacting to an incomplete environmental situation is a derivative of the "releaser" concept developed by Lorenz and by Tinbergen (1948). A releaser is a structure of the environment or a behavior of one animal, which elicits a sequence of behavior by another animal. It is characteristic that the releaser is only a segment of the complete goal-object or goal-situation to which the reacting animal responds. Under usual conditions the behavior of the reacting animal proves satisfactory, since the complete goal-object or goal-situation is actually present. Tinbergen showed that the red belly of male stickleback fish during the breeding season served as a releaser, which elicited the female to follow the male to the spawning ground. Females will follow objects with ventral red areas which only remotely resemble fish in appearance. Under such conditions the behavior of the female can have no effective solution. Admittedly, much research needs to be done in the field of elicitation of behavior of social implication by releasers, but the releaser concept, nevertheless, provides a useful theoretical framework for orienting research.

Harris (1950) has made some interesting studies of spatial orientation in the deermouse, *Peromyscus*, which bears on the problem of the role of "releaser phenomena" on population dynamics. *Peromyscus maniculatus bairdi* inhabits grassland, whereas *Peromyscus maniculatus gracilis* inhabits woodlands. These two closely related subspecies may live in adjoining habitats and yet never interbreed, although they do so freely in the laboratory. Adjoining rooms with an inter-connecting passage were arranged to simulate the natural habitats. "Grassland" was made of bunches of thin strips of heavy paper, while "forests" were simply sections of small trees standing on end. When given a free choice of movement between these two rooms each of these subspecies of mice spent a significantly greater amount of time in the habitat simulating their natural one. Such orientation was just as efficient by mice born and raised in small laboratory cages as it was by mice trapped in the wild. It showed that these mice possess an innate capacity for tropistic behavior for which only a small segment of the environment is required as a *releaser*. This type of behavior is one of the keys as to why animals make differential usage of the available environment—space in particular being considered. Although extrapolating from experimental situations sometimes leads to false conclusions, one would strongly suspect that both the spacing and form of vegetation are important factors in both the occurrence of a deermouse in a habitat and the size of its home range, perhaps irrespective of the supply of food and harborage. Certainly, these ideas present a provocative subject for both observational and experimental studies. In fact, one is led to wonder how the behavior of animals is altered when they find themselves confined, as on islands, to habitats from which they cannot escape and to which their heredity does not permit their proper adjustment. Such an area of investigation might be designated as "*comparative esthetics.*" Its ultimate analysis presumably would concern the manner in which the art forms of the material world about him affect man's behavior and peace of mind. Further theoretical

aspects of releaser phenomena to social behavior have been pointed out by Ginsburg (1949). He says: "What interests me here is that a phylogeny of such releasers amounts to a phylogeny of symbolic behavior and indicates an innate capacity to derive meaning from abstract symbols. It is true that we do not know what this meaning is on an ideational level; nevertheless, it has its counterpart in human behavior if we accept the findings of orthodox Freudians."

The second phenomenon of failure to react to those existing portions of the environment, which potentially should contribute to the well-being of the organism, is one with reverberations in the dynamics of populations. The point involved here is that conditions arise which preclude the organism making the optimum use of available resources, whether they be physical, biological or social. In the field of psychology a large portion of the research in learning theory and abnormal behavior is actually involved with this problem. Likewise, it is the crux of the endeavors of psychoanalysis to reveal the origins of such situations. Field workers in ecology frequently observe animals whose reactions are out of harmony with their environment, and it is one of the aims of wildlife management to prevent their origin. In the experimental field we find such attempts to designate the problem, as in Tolman's (1949) concept of "perceptual blindness," or we find the conditions exemplified in such artificial situations as Liddell's (1942) work in producing "abnormal behavior" in his investigation of conditioned reflexes.

I would like to cite an observation of my own from my free-ranging colony of Norway rats. It exemplifies the complexities which may arise in an open society. Most rats, particularly those which have received mild degrees of punitive action from their associates, stored food in their burrows. The food might or might not be eaten immediately upon taking it to the burrow. Transportation of food in itself might satisfy a drive; however, it is to be noted that these rats deposited the transported food in locations where they themselves would have a good chance of securing it later. On the other hand, the storing behavior of rats who have experienced excessive punitive action from their associates is quite different. Repeated trips would be made from the food hopper depositing food at scattered points nearby, usually not more than 15 feet away, whereas the burrows were all further away. Once this food was left the rats which had done the transporting paid no further attention to it. Whatever the mechanism of development of this behavior may be, it is readily evident that the rats exhibiting it are no longer making a favorable use of this aspect of their environment.

An interesting aspect of this behavior, which is certainly abnormal from the individual's viewpoint, is beneficial with reference to the entire colony. (This type of behavior occurred in less than five percent of over 200 rats observed. Associated characteristics in such rats formed a syndrome which included (1) accentuated pre-weaning competition with older sibs, (2) inhibited growth during entire life span, (3) "freezing" when cornered in a trap or harborage, (4) lack of successful reproduction.) This scattering of the food made it more available and thus reduced competition at the main source of food. This observation

raises the question, "how abnormal is abnormal behavior?" Though an individual rat may have its behavior so disturbed that its own effective reproduction is prevented and its own proper usage of food inhibited, it may, nevertheless, make a significant contribution to the welfare of its society through making the environment more favorable for its associates. For proper evaluation the range of variation in individual behavior needs to be viewed both as it affects the individual and the group.

Perception of spatial relationships and the manner in which animals utilize the space available to them have important social implications and exert a controlling influence on density. Territoriality, the active defense of a given tract, and home range, the occupancy of a preferred area, function as active or passive means of maintaining dispersion of individuals or groups (Allee, *et al.*, 1949, page 412; Burt, 1943; Nice, 1941). Although we lack sufficient knowledge to state exactly why an animal occupies a territory or home range of a given size, one rather general characteristic is that more food exists in the occupied area than is utilized.

This restriction of the privilege of occupying space irrespective of food imposes limitations to population growth not realized by the earlier students of this subject (Davis, 1950). Social hierarchies provide an elaboration to the complexity of territory or home range. The development of rank-order systems permits the organization of group integrity and stability which in turn leads to in-group and out-group status. Attraction between members of a group and antagonism between members of different groups produce local concentrations with intervening buffer zones which are little used by the members of adjacent groups (Keith, 1949; Scott, 1943; and author's observations on rats).

Perception of spatial relationships may have repercussions directly or indirectly on both social behavior and population dynamics, because patterns of locomotion through an environment alter the rate of contact between associates, as well as their orientation to the physical structures of the habitat.

At the Jackson Laboratory litters of dogs are raised in 20 x 70-foot pens. Snow trails reveal the manner in which the dogs utilize their confined area. Wirehaired Fox Terriers beat a single path about the periphery; Cocker Spaniels also beat a path about the periphery of the pen, but they also beat a few trails diagonally across the pen; Beagles and Basenjis form trails as do Cocker Spaniels, but in addition there are occasional to frequent wanderings away from the paths through the otherwise unbroken snow; and finally, the opposite extreme from the Wirehaired Fox Terriers is exhibited by Shetland Sheep Dogs—their tracks appear to be distributed completely at random over the pen with very little indication of a peripheral trail adjacent to the fence. Of course, we do not know what sort of natural population these breeds are capable of developing, but the snow-trail patterns exhibited indicate that these breeds would markedly differ in their utilization of their home range.

Another factor which has direct implications for population dynamics, particularly among social species, is that of *preadaptation* (Allee, *et al.*, 1949, page 642). Although natural selection may have been operating on a species with

the result that this species exhibits the ability to make an optimum adjustment to some particular environment, the species may, nevertheless, make a very excellent adjustment to some new environment with which it has had no prior association. In fact, some animals prosper in the new situation, as indicated by expansion of the population into new areas or by increases in density. Such adaptation is particularly prominent among such birds as robins, chimney swifts, bluebirds, wrens, and kingbirds (Kennedy, 1915), which have utilized many man-made structures to increase their available nesting or feeding niches. This same utilization of environments, highly altered by man, is especially exhibited

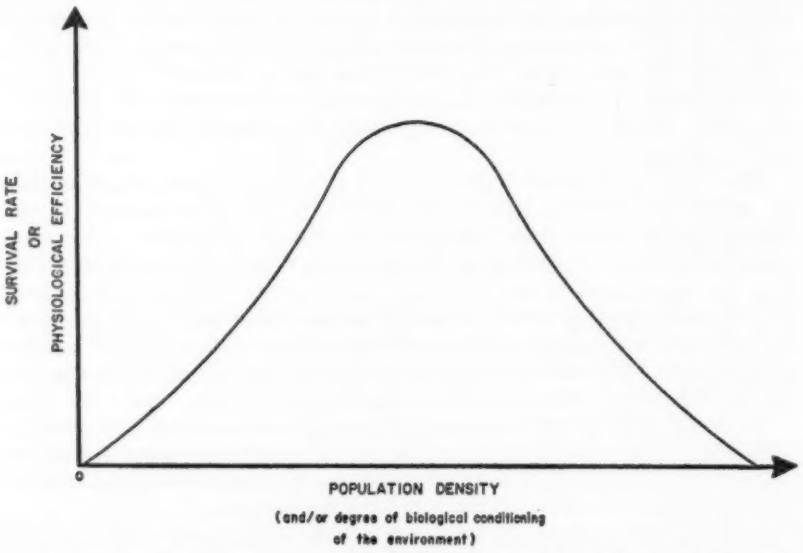

FIG. 1.—The relationship of population density to biological activity (after Allee). It is through the operation of this principle that sociality influences the rate of individual growth, biotic potential of population growth, and the permutations of behavior.

by such forms as the house mouse and the Norway rat. Preadaptation phenomena include the ability to engage in complex behaviors in entirely new situations. Under the artificial environment of the laboratory myriads of experiments with the derived strains of the Norway rat have amply demonstrated this ability. Under completely free-ranging conditions ground squirrels will engage and solve many intricate problems presented to them in their normal environment (Gordon, 1943).

The phenomenon of preadaptation becomes of particular importance when the opportunity for it to be exhibited occurs in a population characterized by cultural continuity. Although the original manner of exploitation of a new environmental situation may be by chance, by learning, or by reasoning, its

continued contribution to the welfare of the population is greatly enhanced by the new patterns of behavior being passed on to later generations through cultural processes. In time, the behavior may be further elaborated, so as to further the biological conditioning of the environment and also to modify the cultural pattern. In the long run, what preadapted and culturally modified behavior does is to permit the population to make more effective use of available energy. A striking example of this is reflected in the population growth (Fig. 2) of Germany (Dewey and Daikin, 1947). One cycle of growth during an agricultural economy

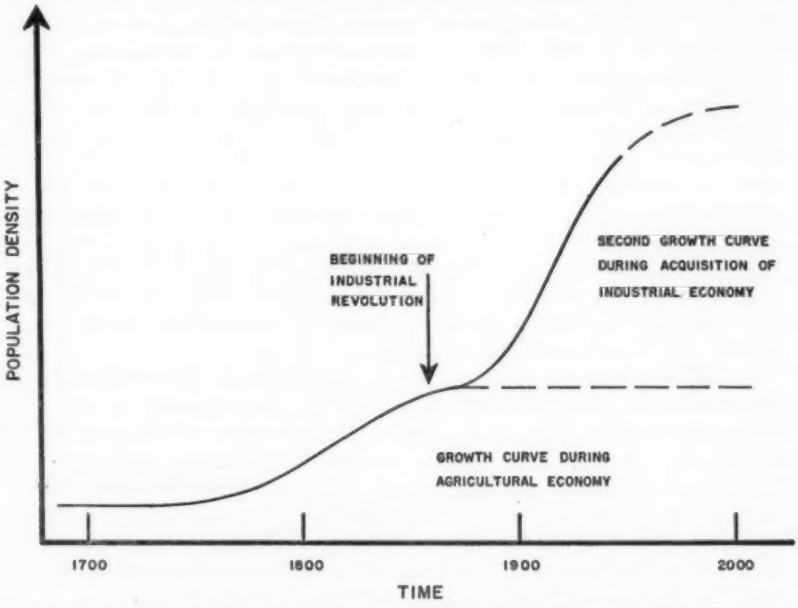

FIG. 2.—Population growth in Germany (after Dewey and Daikin). This figure typifies the influence upon the resultant population growth of the ability of an organism to utilize the available energy. Such changes in ability may arise through either genetic or cultural changes within the species.

had just about terminated at the beginning of the industrial revolution. At that time there arose a new growth curve which has only recently approached completion. Thus, the carrying capacity of an environment must also be considered from the ability and opportunity of its inhabitants to exploit the available energy. Each new type of exploitation gives rise to a heightened level of population density. (Many similar examples could be cited utilizing infra-human animals. An outstanding one is that of the chimney-swift. Prior to the arrival of white man in North America it nested in hollow trees, and during the migration seasons they aggregated in fairly large flocks which spent the night together. With the replacement of hollow trees by myriads of chimneys as a nesting

niche, the abundance of this species has greatly increased. In addition to the increase in social contacts imposed by the proximity of chimneys, much larger aggregates—at times reaching many thousands—are formed in chimneys of large buildings during migration. Similar phenomena are characteristically observed in the changes of population densities during the succession of plant and animal communities (Allee, *et al.*, 1949). Animals or plants characteristic of a later stage of succession are commonly found as scarce invaders of an earlier stage. As the community structure changes and as conditions become more favorable for the invader its numbers increase. An important aspect of this situation is that the organism participates in the production of an environment more favorable to itself. From a research viewpoint the investigation of this phenomenon resolves itself into two aspects: (1) In what ways do organisms alter their environment to make them more favorable? (2) How can animals be induced to make more rapid and more efficient alterations and yet maintain their cultural stability?) The repetition of this process requires continued increase in complexity of the social organization. And as has been previously remarked, after a time there are continued restrictions to the development and expression of behavioral potentialities—a process, which we may anticipate, will terminate with the individual being only a hollow shell of his potential self. Opportunity for free expression of hereditary potentials of behavior and the drive toward increased utilization of available energy by the group are in part complimentary and in part conflicting tendencies.

Natural selection toward the survival of organizations of life which make more effective use of available energy is exhibited in the succession of plant and animal communities (Allee, *et al.*, 1949). The final stages are characterized by an increased rate of energy intake from the sun (by plants), by an increased rate of release of free energy (particulary by animals), by greater complexity of organization, and usually by a greater weight of living matter per area. In our search for guide posts for human civilization we would do well to examine more closely the dynamics of community succession whose terminal stage is self perpetuating as long as drastic changes in climate do not occur.

Nor can we consider the utilization of available energy without taking into account the growth of a population (that is, its density) with reference to the growth of the individual members of the population. Fishery research has shown that in a given body of water a relatively large number of stunted fish or a much fewer number of large fish may live. Density cannot be considered irrespective of the welfare of the individual. If the rat is at all typical, mammals behave much as do fish. In my Towson colony of Norway rats, as the population increased, more and more individuals were physically stunted despite having plenty of food available. Such stunted rats seemed healthy, as judged by the occurrence of fat—they simply failed to grow very large and attained their mature weight very slowly. These stunted rats were characterized by behavioral disturbances imposed by the increasing complexity of the social structure. Dwarfism or abnormal growth in man may also be associated with behavioral disturbances arising from unstable social environments (Binning, 1948; Fried and Mayer. 1948; Talbot, *et al.*, 1947).

Thus, we see that several growth processes are closely interrelated: (1) the rate of physical growth and skeletal maturation in the individual, (2) the level of mature growth of the individual, (3) the level of sexual and behavioral maturity in the individual, (4) the degree to which an individual or group is enabled to express genetic potentialities, (5) the growth rate of a population and its density at maturity, and (6) the social integration of a population—all these are inter-dependent variables whose expression is in turn influenced by the structure of the environment and the degree of cultural continuity possible.

The extent to which one of these growth phenomena may be enhanced through the partial suppression of the others raises the problem of value systems. Population density may be intensified at the expense of reduction in individual growth, and an increase in social tension. Maximum individual growth may be assured, through isolation with the resultant induced social sterility, irrespective of population density. A realization of the interdependence of these growth phenomena provides the viewpoint for the establishment of a truly comparative science of sociobiology.

As our human society becomes more highly technical, there arises the tendency to accentuate one of these growth phenomena without any consideration as to its effect on other aspects of life. This is particularly so as regards increasing population density, which in many quarters is accepted as a desirable objective. Bateson (1912) long ago realized the fallacy of this concept when he said: "It is not the *maximum* number but the *optimum* number, having regard to the means of distribution, that it should be the endeavor of social organization to secure. To spread a layer of human protoplasm of the greatest possible thickness over the earth—the implied ambition of many publicists—in the light of natural knowledge is seen to be reckless folly."

Yet such accentuation of a single aspect of the value systems relating to growth phenomena continue. E. G. Rochow (1949) predicts that it will be possible to feed a population of one billion persons (this is over five times the upper level indicated by the present trend) living within the boundaries of the United States. In a letter to me, Dr. Rochow made this further elaboration: "The chief difficulty arises, of course, in feeding so large a population, particularly if it is to spread over and inhabit a large part of the present farm lands. This is the part of the problem that becomes a challenge to chemists" and "I should also like to point out that the high population density in large cities is in part alleviated by purposeful isolation of many of the inhabitants." The choice before us is to develop a society whose numbers are limited, but whose members live a full life, or, as Rochow believes, to develop a society of maximum numbers whose members have had a restricted experience accompanied by an inhibition of many potentialities of expression. Maximum production of protoplasm is a valid concept and objective in the field of animal husbandry, but it is of doubtful value when applied to human society or even to game management. Current discussions of increasing agricultural production are also frequently so worded as to imply that what is possible is desirable—with little critical thought as to the consequences on the human population.

In this whole problem of the social aspects of population dynamics an im-

portant consideration is the individual's learning the nature of his physical and social environment. Although some behavior does not reach full development until an animal is quite mature, such as copulation and defense of territory, nevertheless, most contacts that an animal has with his environment begin very early in life. In fact, even where the complete behavior pattern or the full experience only occurs during adult life, the experiences of infancy and the juvenile period markedly alter later life (Hymovitch, 1949). The learning process among immature animals is qualitatively different; where the young are prevented from perceiving the environment, they, as adults, do not profit as well from similar experiences. Experiences during early life have a profound effect upon adult behavior and health. These conclusions apply to both physical and social aspects of the environment. Among dogs the latter part of the nursing period and the period just following weaning form a brief but critical one for the development of social adjustments (Scott and Marston, 1950). My own observations on wild rats were not such as to result in any clear-cut conclusions regarding the role of pre-weaning experience, but they amply demonstrated that the immediate post weaning and preadolescent periods were critical for future development. Among these rats social status, rate of growth, adult size, and stability of behavior were in large part determined during this juvenile period. In our observations of animals under natural conditions, in experimental studies of population ecology, and in laboratory studies of isolated animals or small groups, we need to give increasing attention to the manner in which the environment and experience of juvenile animals affect their behavior as adults.

In all species, regardless of their degree of sociality, natural selection operates on all levels of organic complexity from the individual to the population (Allee, 1945). *By a population we mean: any contiguously distributed grouping of a single species which is characterized by both genetic and cultural continuity through several generations.* Therefore, if we are to make real progress in understanding the interrelationships of sociality and population dynamics, our observations need to be focused upon the population as the major unit in which the lives of individuals find reality. Particular stress needs to be laid upon those factors which alter the maturation of the individual on the one hand, and, on the other, to the variations in the structure of the environment, which mold the fate of both individuals and populations. From an experimental standpoint this means that we must use populations as our experimental units; these to be followed from their inception with a few members to the maturity and possible senescence of the population, and to be studied in environments where many of the physical factors of the environment are controlled and organized into meaningful patterns. Fuller (1950), in his Situational Analysis, has provided a framework for the experimental manipulation of the field parameters of behavior (incentive, barriers, and complexity) into meaningful patterns. This framework coupled with Calhoun's (1950) approach to the experimental manipulation of population as the unit of investigation presents the necessary background for objective investigation of the social aspects of population dynamics. Many helpful suggestions for plan-

ning experimental studies of sociality are included in the "Minutes of the Conference on Genetics and Social Behavior" (Scott, 1946).

In the planning of such experiments we may rely on the great wealth of ecological field observations and the equally great wealth of laboratory studies of the psychology and physiology of individuals and small groups. At best, experimental studies into population dynamics, even with those vertebrates characterized by high reproductive potentials, take several years for completion. They require substantial sums of money and should be pursued simultaneously by investigators trained in several diverse disciplines. To be sure, this is a large order, but small in comparison to the likely contributions to the welfare of man and the world about him. Any interpretation of results pertaining to the interrelationship between sociality and population dynamics involves judgment values. This is as it should be. However, such judgment values can only gain reliability when viewed against a background of experimentation, which enables manipulation of the variables, as well as repetition of experiments with the view of determining the variability of the end results of social equilibrium, when the accompanying static aspects of the environment (and heredity) are maintained constant.

Initial studies under controlled conditions of the interrelationship between sociality and population dynamics are likely to be most fruitful if we utilize some of the common experimental mammals and their wild counterparts. Of these the most useful will be: (1) the mouse, *Mus musculus;* (2) the rat, *Rattus norvegicus;* (3) the rabbit, *Oryctolagus cuniculus*, (4) the dog-wolf complex, *Canis lupus;* and (5) the rhesus monkey, *Macaca mulatta*. This arises from the fact that there is a great backlog of biological information concerning them, and that scientists in several biological disciplines are accustomed to working with these forms. Four of these forms (mouse, rat, rabbit, and dog-wolf) are particularly suitable, since for them there is available a large number of highly inbred strains or genetically divergent breeds. This variability may be used to exploit the heredity parameter of the organism-environment complex. Scott (1949) has discussed in detail the value of inbred strains for experimental work relative to behavior, and Heston (1949) has similarly treated the usage of inbred strains in physiological studies. Inbred strains or breeds exhibit accentuation or inhibition of behavior characteristic of the wild form. It is this type of variability from the wild type which makes the use of such genetic derivatives useful. On the primate level we should have available breeds or inbred strains of a species suitable for use in the laboratory and in the field situation required by experimental population ecology. The rhesus monkey (Carpenter, 1942) is probably most suitable for such genetic work leading to further behavior studies. Although I have mainly stressed environmental influences in the present discussion, we must bear in mind that an analysis of the social aspects of population dynamics must be based upon a consideration of both heredity and environment. Sumner (1922) long ago ably pointed out that, insofar as the existence of life was concerned, neither heredity nor environment had reality in the absence of the other.

It so happens that all five of the species are characterized by rather complex social structure in comparison with many other representatives of their orders. To produce the fullest understanding of sociality and population dynamics some of those species with less complex social structure should also be thoroughly investigated.

Although present knowledge, derived from ecological studies of animals living in their native habitat, and from psychological studies of animals in the semi-isolated unsocial conditions of the laboratory, gives us a firm foothold for planning controlled studies of population ecology, much additional basic information is desirable. We particularly need many more detailed life-history studies of animals in their native habitats. These will be most effective when parallel life histories are made comparing related species known to differ in social structure. In practically all orders and many smaller taxonomic categories

TABLE 1.—*Comparative degrees of sociality between related genera*[1]

COMMON NAME	ORDER	SLIGHTLY SOCIAL	MORE HIGHLY SOCIAL
Deer	Artiodactyla	Moose (*Alces*)	Elk (*Cervus*)
Rabbits	Lagomorpha	Cottontails (*Sylvilagus*)	European rabbit (*Oryctolagus*)
Rodents	Rodentia	Deermouse (*Peromyscus*)	Norway rat (*Rattus*)
Opossums	Marsupialia	American opossum (*Didelphis*)	Australian opossum (*Trichosurus*)

[1] Literature references: Moose (Denniston, 1949); elk (Altmann, 1950); cottontails (Trippensee, 1934); European rabbit (Southern, 1940, 1947); deermouse (Howard, 1949; Nicholson, 1941); Norway rat (Calhoun, 1949*a*, 1949*b*); American opossum (Lay, 1942); Australian opossum (Pracy and Kean, 1949).

of mammals, there exists a wide range in the degree of sociality between different species. Table 1 presents examples of the wide range of sociality existing between related genera. In each instance the degree of sociality is judged on the basis of the size and permanence of groups, as well as the complexity of interrelationships between individuals and groups.

The existence of wide ranges of sociality among many groups of mammals, even including the primitive marsupials, makes it highly likely that determination of social structure is in large part independent of the degree of evolution of the cerebrum.

Investigation of the following topics by those making life history studies will be most helpful in bringing about a better understanding of the relationship between sociality and population dynamics.

1. What are the goal-objects toward or between which animals orient?
2. How are these goal-objects distributed through space and time, particularly as they relate to the energy expenditure of the organism in re-encountering a goal-object?

3. What are the physical barriers of the environment and the complexity of their arrangement, which modify the likelihood of an animal perceiving or reaching a goal-object or of contacting other individuals?
4. What are the pain-producing barriers (both physical and social) which may occur between an animal and its goal-object?
5. How are the physical barriers or the pain-producing barriers distributed through space and time?
6. Describe each observed type of behavior in terms of:
    A. Composition of group involved (sex, age, relationship, etc.—see especially Carpenter, 1942).
    B. Type of behavior as regards its origin and function (see Scott, 1946, p. 23).
    C. Innate drives whose satisfaction depends upon the occurrence and distribution of goal-objects and barriers.
7. What are the conditions of juvenile life as related to:
    A. Relative maturity at birth.
    B. Length and pattern of dependency of young upon their mother or other associates, including frequency and kind of contact.
    C. Manner in which the young are integrated into the social structure.
    D. The maturation of each goal-object oriented behavior.
8. In what ways do the animals biologically condition their environment, and how does such conditioning influence the expression of either innate or learned behavior?
9. What is the social structure of groups in terms of rank-order relationships or other inter-individual adjustments?
10. What is the pattern of relationships between different groups?
11. How is the growth of the individual, its reproductive success, and likelihood of survival associated with the above types of data?

Whereas, other types (refer to the outlines appearing from time to time in Ecology, whose publication is sponsored through the Committee for Life History Studies) of observations are useful in preparing life history studies, the systematic accumulation of data of the above type will be of great usefulness in the next step of analysis—the planning and execution of controlled experimental studies into population ecology. Such data will facilitate a systematic arrangement of environmental components. In the native habitats of most animals goal-objects, barriers, and other physical structures are so irregularly arranged as to enable us to arrive at only vague approximations of their influence. From these life history-derived approximations we may logically plan the arrangement of goal-objects, barriers, and the like so that we may derive general principles as to their influence on population dynamics, social structures, and evolution of culture.

Concepts and techniques developed in the science of psychology will also be of great usefulness in planning and conducting experiments in population ecology. In its development, psychology has relied mainly on clinical studies of man and of experimental studies of various laboratory animals, the latter under

essentially unsocial conditions. Both of these approaches are atomistic in the sense that they must perforce view the individual, whose past history and environment is little known, or which is living essentially out of context with its natural physical and social environment. Nevertheless, these two psychological approaches have given us great insight into the manner in which the individual perceives, learns, and adjusts, and to a more limited extent it has shown how individuals react to and with others of their kind in rather simple stereotyped environments. The time is now ripe to utilize this great host of information in planning experiments and analyzing results in which the unit of investigation is the population.

The potential contribution of psychology to the investigation of the behavioral aspects of population dynamics may not be realized by current trends in psychological research. Psychology has stressed the development of concepts at the expense of the descriptive aspects of behavior. Such comparative psychological endeavors can provide a cataloging of the range of behavior exhibited by a species and of the range of conditions which elicit such behaviors. Such data needs to be available both for the wild-type representative of each species and also for genetically similar isolated groups of the species, such as subspecies, inbred strains, or breeds. Such descriptive studies will form the building blocks of behavior with which we can proceed with greater assurance in planning experimental studies into group dynamics and population ecology.

With each new increase in complexity of life new properties arise, and the phenomena exhibited by the less complex forms of life take on new meaning. Thus, our knowledge of the behavior of individuals and small groups will assume richer connotations and reveal new concepts when applied to the social population level of organic organization. In turn, it is inevitable that investigation at this level of organization will produce new topics for investigation under strictly laboratory conditions.

Concepts of the social aspects of population dynamics are of potential value to three spheres of human activity. They contribute to man's management of himself through the development of a "preventive medicine" of mental hygiene, through its contribution to psychiatry by providing a better appreciation of the relationship of the total individual to his total environment (Cameron, 1948); through the provision of principles of community planning; and through the assessment of desirable population densities. They contribute, in the sphere of animal husbandry, to man's management of domestic animals, so that they will most economically provide him with sustenance. They contribute to the essential problem of man's management of the world about him in the broad fields of conservation and wildlife management; for man lives not alone, but in context with the "balance of nature," which he disrupts at his own peril. Admittedly, the concepts of the social aspect of population dynamics are as yet in an embryonic state. Their development to the point where we may safely and surely apply such knowledge presents a challenge to research. To meet this challenge we must plan long-term observational studies of the social ecology of man and other animals under their normal conditions of existence; we must plan long-term ex-

perimental studies of population ecology where conditions of the physical environment, which mold social structure, are systematically controlled, and where the history of the population is followed through the years from infancy to maturity; we must have the courage and foresight to depart from the laboratory in its customarily accepted sense, and take with us into the broader laboratory of field situations our extensive knowledge derived from analytical studies of the individual and small groups. Such procedures will lend greater insight into the dynamics of group behavior as well as provide new problems to carry back with us into the laboratory for other analytical treatment.

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WINTER POPULATION OF PINNIPEDS ABOUT GUADALUPE, SAN BENITO, AND CEDROS ISLANDS, BAJA CALIFORNIA

By George A. Bartholomew, Jr., and Carl L. Hubbs

Between January 27 and February 10, 1950, as guests of Joseph W. Sefton, Jr., a scientific party, including the authors, visited Guadalupe, San Benito, and Cedros islands aboard the Research Ship *Orca* of the Joseph W. Sefton Foundation. The primary purposes of this trip were to determine if there still exists on Guadalupe Island a population of the Guadalupe fur seal, *Arctocephalus townsendi* Merriam, of which a single adult male had recently been seen on San Nicolas island, California (see below), and to study further the numbers and biology of all the pinnipeds on these Baja California islands. Records were made of all individuals seen at sea and censuses were taken of the pinniped populations on each island. These observations yielded a hitherto unavailable picture of the winter population in this area.

No harbor seals, *Phoca vitulina geronimensis* Allen, were seen on any of the islands, although according to Goldman (1951: 407) they still occur on Guadalupe Island. We have found no confirmation of this report.

GUADALUPE ISLAND

A fortunate combination of good weather, co-operative personnel and continuous access to boats well adapted to our purposes made it possible to examine, with considerable thoroughness, the coastal areas of Guadalupe Island, particularly on the south and east sides (Fig. 2).

On the *Orca* we completely circumnavigated this oceanic island, cruising close to the shore and recording the numbers, kinds, and locations of all marine mammals seen. Twice one of us (Bartholomew) examined every nook and cranny of the east coast between Melpomene Cove and a point six miles north of South Bluff in one of the *Orca's* motor launches, skillfully operated by A. A. Allanson of the Scripps Institution of Oceanography. Four days were spent ashore, two and a half at West Anchorage and along the adjacent coast both north and south, one along the southern part of the east coast, and a half day on the beaches south of Pilot Rock. Outer Islet was visited twice and the area about the anchorage in Melpomene Cove was under almost continuous surveillance. We feel that the counts resulting from these efforts rather accurately indicate the numbers and kinds of Pinnipedia on Guadalupe Island during the visit.

Zalophus californianus (Lesson). California sea lion.—For the past half century, during which counts have been made at irregular intervals, the population of sea lions on Guadalupe Island has always been small, in comparison with the great concentrations about the islands and rocks nearer the mainland. Townsend (1899) reported that the only sizable aggregation which he saw on circumnavigating the island in June, 1892, was a group of about 30 hauled out on Outer Islet. As a result of his search for pinnipeds about Guadalupe in June, 1897, Thoburn (1899) similarly indicated that the only large group of sea lions found was a herd on Outer Islet consisting of 10 bulls, 50 cows, and 31 pups. After a week's circumnavigation of the island, in July, 1922, Anthony (1925: 304) reported that ". . . one rookery of a dozen was found and a few scattered individuals along the shores that might have made the Guadalupe count as much as 50 animals."

During the period of our visit the *Zalophus* population, although larger than previously reported, was still of modest size. In addition to five individuals seen at one time or another off the east and west sides of the island, sea lions were found in only two areas. The largest single group hauled out regularly on the ledges along the west and south sides of Outer Islet. It contained a minimum of 134 animals, largely adult females and young males; only 3 adult males and 12 yearlings and young-of-the-year were seen. The other concentration of *Zalophus* was near the north end of Guadalupe. On February 3, a half dozen were observed near Pilot Rock and about 20 otariids, presumably *Zalophus*, were seen from a distance about one-fourth mile off the north shore.

The observed scarcity of yearlings and young-of-the-year in the herd on Outer Islet is what one would expect in a stable or decreasing population. The small size and stability of the *Zalophus* population of Guadalupe is of particular interest because of the availability of an extensive and relatively unexploited habitat apparently suitable for sea lion occupancy. The abandoned fur seal rookeries harbored not a single *Zalophus* at the time of our visit. Clearly, the small size of the population is not attributable to any inadequacy of the hauling grounds. Nor can we plausibly attribute the low numbers to lack of food, for we have found the local waters to abound in fishes. Neither can we assume that the sea lions' scarcity is related to the abundance of other pinniped species, for the numbers of fur seals have long since been reduced to insignificance and the cohabitation of elephant seals (now abundant) and sea lions is attested by their free sharing of rookeries on San Benito Islands (see below) and on Los Coronados and San Nicolas islands to the northward.

The long persistence and integrity of the Outer Islet colony, despite its small size and the very limited hauling ground (a narrow shelf on a nearly vertical face), is attested by the long record of a moderate proportion of albinistic individuals in this population. These "albinos" have been well known to the biologists who have visited the island from time to time during the past quarter century. Some were seen by us. Others are shown on a color photograph taken by George E. Lindsay in 1948. Lewis Wayne Walker (personal communication) estimates that the "albinos" have constituted about ten per cent of the small population on each of his several visits during the past twenty years. He further states that William E. Clover, who rediscovered the fur seals on the island, and Dr. Harry Wegeforth, when President of the San Diego Zoological Society, and also Luis Camillo and others, often spoke of seeing albinos on the south side of Outer Islet repeatedly from 1926 to about 1935.

Why the sea lions on Guadalupe Island have failed to take over the abandoned fur seal rookeries is a mystery, especially since the sea lions on the San Benitos now occupy all available sites, some of which originally must have been utilized by the fur seals that, as Anthony (1925: 308) has shown, once abounded there.

A possible explanation for the scarcity of sea lions on Guadalupe is that some of the environmental conditions on this truly oceanic island, which rises abruptly out of very deep water, do not satisfy the full needs of this essentially coastal animal. The other islands inhabited by *Z. californianus* are surrounded by the continental shelf.

Arctocephalus townsendi Merriam. Guadalupe fur seal.—The discovery during the summer of 1949 of an adult male of *Arctocephalus townsendi* on San Nicolas Island, California (Bartholomew, 1950) led us to expect that a population of this once wide-spread species might persist on Guadalupe Island, which was its last major holdout (Starks, 1922; Anthony, 1925; Townsend, 1931). It was on this island that the species was rediscovered in January, 1926, after it had been long thought to be extinct.

An intensive search for *Arctocephalus* was therefore made about Guadalupe Island throughout our stay. In this effort we were materially aided by testimony furnished to Joseph W. Sefton, Jr., and one of us (Hubbs) by Harry Fisher, just before his death. Fisher was the partner of William E. Clover and the fellow rediscoverer of the fur seal.

An entire day was spent ashore in a minute examination of the stretch of coast identified by Fisher as the area where the fur seal was rediscovered and where he thought that Clover, in 1928, captured the two male specimens that were brought to the San Diego Zoo

(Huey, 1930; Bartholomew, 1950). This site was given as being on the east shore about four miles north of the south end of the island, and as being marked by a double point with a

PLATE I

The inland edge of an abandoned fur seal rookery on the south end of the east coast of Guadalupe Island, showing the polish imparted to the rocks by the movements of generations of fur seals, and the abrupt transition from polished to unpolished rock.

small rock pinnacle off the southerly tip. Such a point was found at the indicated position. Between the points there was a cave with a covered entrance corresponding to the description given by fishermen (Fisher, Clover, and Luis Camillo) of the cave which the fur seals entered and where the Zoo specimens were netted.

From the testimony of Fisher and others it seems highly probable that a small residual population existed along this section of the east coast of Guadalupe Island for several years

following the rediscovery in 1926. Fisher recalled having counted 31 here and he said that neither he nor Clover found any elsewhere. He admitted having shot two, but did not dis-

PLATE II

A view of part of the herd of elephant seals on the beach south of Pilot Rock, Guadalupe Island.

close their disposition. Lewis Wayne Walker, who made several trips to Guadalupe Island with Dr. Harry Wegeforth following the capture of the two specimens in 1928, recalls having seen individual fur seals several times at the supposed point of rediscovery, but he thinks that the observations were made only about one-third the way down the east coast from the north end of the island.

The long-abandoned fur seal rookery at West Anchorage was carefully watched for two and a half days and several visits were made to the other abandoned rookeries, at Melpomene Cove and on the east coast several miles north of South Bluff. In addition, re-

peated searches were made from a launch elsewhere along the east shore and a watch was maintained as the *Orca* cruised along the northern and western as well as along the eastern shores.

None of these efforts yielded any indication of the presence of fur seals on Guadalupe Island either now or in the recent past. The old fur seal rookery at West Anchorage, marked not only by rocks polished to a high sheen by generations of fur seals (Pl. I), but also by crumbling stone huts built in the days of the Russian fur trade (Anthony, 1925), is now occupied only by a small herd of elephant seals. The rookeries at Melpomene Cove and on the east coast, also marked by polished rock, remain completely unoccupied and do not appear to have been recently inhabited by any pinnipeds.

Since we were unable to search the north and northwest parts of the island with the same degree of attention that we devoted to the east and south coasts, it would be presumptuous to state categorically that during our visit there were no fur seals on Guadalupe. We can say with considerable confidence, however, that there were none on the west side of the island south of a point three miles north of West Anchorage and none on the south or east sides of the island. It is possible that the adult male seen recently on San Nicolas Island (Bartholomew, 1950) was the last living remnant of a once flourishing tribe.

Mirounga angustirostris (Gill). Northern elephant seal.—Since the rediscovery of the northern elephant seal on Guadalupe Island in 1892 (Townsend, 1899), the population of this species has been of interest to mammalogists and conservationists. What little was known of the population increase from 1892 to 1929 was summarized by Huey (1930). Although a number of biologists have since visited the island no further censuses have been published, except the 1948 count of Fitch and Wilson (1949).

Despite the meagerness of the data and despite the circumstance that the various counts have been made at different times of the year, and have thus covered considerable seasonal fluctuations in the number of animals on the island, the available censuses indicate a definite and spectacular increase over the last decade or two (Fig. 1). The increase has been so marked that the errors in sampling do not obscure the basic picture.

The northern elephant seal was brought to the brink of extinction by commercial hunting. When the population reached such a low point (probably less than 100 individuals) that hunting was no longer profitable, commercial exploitation, of course, stopped. Before the population had again become large enough to be economically attractive the Mexican Government extended protection, under which the small herd has prospered. The species, when it was accorded almost complete protection from the one agent, man, which nearly caused its extermination, multiplied rapidly in the unoccupied niche to which it was adapted. Neither poaching for "trimmings"—male genitalia dried for export to China for the preparation of an aphrodisiac drug (Beebe, 1942)—nor the occasional wanton shooting by visiting fishermen (an instance of which we observed at Melpomene Cove in 1950) has been effective in preventing the increase of the population.

The conditions for population increase seem to have been almost as optimal as in a laboratory study, in which a small known number of organisms is introduced into a most favorable environment. The growth curve shown by the population from 1892 to 1950 (Fig. 1) indeed approximates the lower part of the logistic curve to which the growth of most experimental populations can be fitted. There was a slow initial increase in the years following 1900, but as the population grew the rate of increase became progressively greater. During the last two decades the numbers have increased prodigiously. There are no indications, however, that the curve has approached its point of inflection. If conditions remain as favorable as they now are, we can expect that the population of the species will continue to build up at an increasing rate and will not approach its asymptote until it has increased several-fold. The species has only begun to expand into its previously occupied range and still has an enormous, largely unoccupied habitat available, in California as well as in Baja California.

In any event, the more than 4500 elephant seals that were present on Guadalupe Island during the period of our visit represent by far the largest population of this species that has

ever been recorded from the island. Plate II offers graphic evidence of the abundance of these animals on one of the beaches.

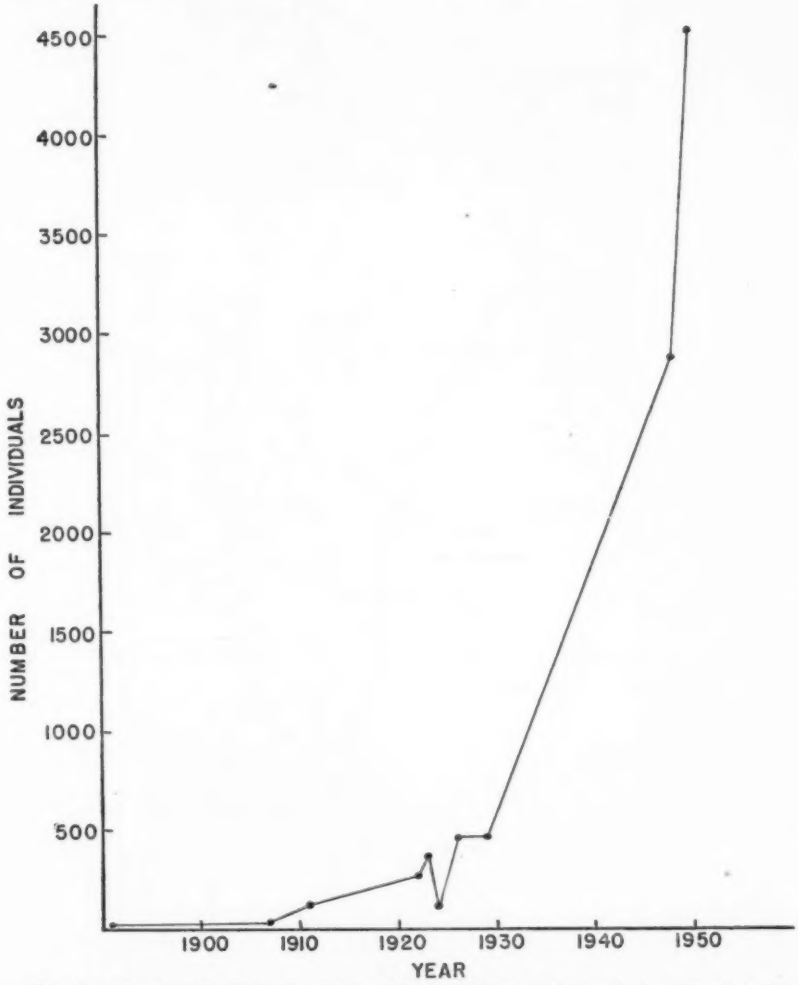

FIG. 1.—The growth of the Guadalupe Island elephant seal population. The data for the years prior to 1930 are from Huey (1930) and the data for 1948 are from Fitch and Wilson (1949).

Associated with this increase in numbers has been a change in the distribution of elephant seals on Guadalupe Island. During the early years of the present century, the animals were found only on the beach south of Elephant Rock. Now, at least during the winter, as can be seen from Fig. 2 and also from the figure in the paper of Fitch and Wil-

son (*op. cit.*), the animals are scattered widely along both east and west sides of the northern part of the island and a sizable herd is established at West Anchorage.

FIG. 2.—The distribution of elephant seals on Guadalupe Island during the last week of January and the first week of February, 1950. The number of animals on the beach south of Elephant Rock was approximated by a rather distant observation. The number on the beach south of Pilot Rock was determined by counting and by analysis of a series of photographs, of which Pl. II is an example.

SAN BENITO ISLANDS

The abundance of pinnipeds on the San Benitos at the time of our visit was well-nigh unbelievable. Over long stretches of coast, every available bit of beach

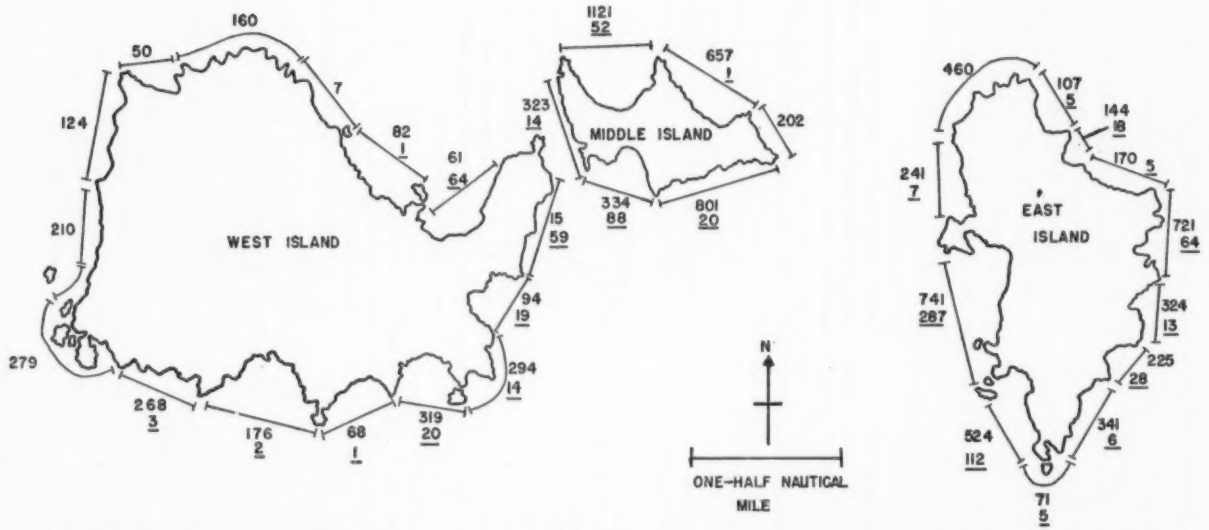

FIG. 3.—The distribution of pinnipeds on the San Benito Islands on Feb. 5, 1950. The underlined numbers indicate elephant seals. The numbers without underlining indicate California sea lions.

and rock was occupied by elephant seals or by sea lions, and groups of the latter were congregated on barren areas 100 feet or more above the water and as far as 150 yards from the shore.

On February 5, with the help of A. A. Allanson and Frederick H. C. Taylor of Scripps Institution, we circumnavigated each of the three small islands of the San Benitos group in a launch. We cruised inside the kelp and just outside the surf, examining every foot of the shore and counting on hand-talley counters all pinnipeds seen in the water and on the land. The numbers in each of the coves, beaches, and headlands were recorded on charts. Since the numbers (Fig. 3) represent animals actually seen, the totals are minimum figures for the pinniped population of the San Benitos.

Zalophus californianus (Lesson). California sea lion.—In the first part of February, 1950, the San Benito Islands were literally overrun with sea lions. Despite their magnitude, the numbers shown in Table 1 and Fig. 3 suggest only feebly the overwhelming abundance of these animals, which swarmed like huge maggots over and around all three islands.

We counted 9714 individuals of *Zalophus* on the three small islands (Table 1) and there can be little doubt that the population at the time of our census was actually well in excess of 10,000. An appreciation of the large size of the San Benitos *Zalophus* population in February, 1950, can be gained from the fact that it was over three times as large as the largest total summer population of this species indicated for the entire State of California by the censuses of the California Division of Fish and Game from 1927 to 1948 (Bonnot and Ripley, 1948).

During the last half century the sea lion population of the San Benitos has not always been at this high level. In March, 1911, only 1700 were found there (Townsend, 1916) and in August, 1922, the population was estimated at 400 (Anthony, 1925).

The size of the sea lion population of the San Benitos is of particular interest because in 1939 an American company killed a large number of the animals on the islands for conversion to dog food. The exact number of animals slaughtered cannot now be determined, but apparently it was very great. Beebe (1942) stated categorically that all sea lions on the San Benitos were killed, but the San Benitos lighthouse keeper, in a conversation with Mr. George E. Lindsay, of the *Orca's* scientific party, estimated that about half of the animals on the islands were killed.

According to Kenneth E. Stager (personal communication), who visited the islands in March, 1940, there were at that time fewer than 2000 sea lions on East Benito—less than half as many as when we visited the same island in February, 1950. At the time of our visit the sea lions appeared to have largely recovered from the killing and there is reason to believe that the population is still increasing.

Lindsay, who collected plants on all three of the San Benitos, pointed out to us vegetational evidence that the sea lion population of the islands was at a higher level than it had been in the years immediately preceding 1950. One of the conspicuous plants on the San Benitos is a soft cactus, *Mammillaria neopalmeri*, which, over considerable areas, particularly on Middle Island, has established itself as the dominant plant. In the San Benitos, the sea lions move 150 yards or more inland to congregate in groups of several hundred individuals. In their movements overland, the sea lions have denuded the ground of most of the plants and have, over considerable stretches of terrain, worn the spines off the *Mammillaria*. Recently in some areas many of the cacti have been uprooted. Under such mechanical abuse, the cacti could never have established themselves as seedlings. Therefore, at the time when they did establish themselves in areas near the beaches, the sea lion population must have been much smaller than it now is.

That the San Benitos sea lion population is still expanding is further indicated by the observed preponderance of young animals. At least three out of four and possibly four out

of five of the sea lions in the San Benitos were less than three years old and the large majority were less than one year old.

Although extremely different in structure, the sea lion populations on Guadalupe and on the San Benitos agreed in the conspicuous absence of adult males. Of the 9714 sea lions which we counted on the San Benitos, only 11 were identified as adult males. Similarly on July 29, 1949, when Dr. J. L. McHugh estimated the population of Middle Island alone as 5000 (our count for this island was 3438) he observed very few adult males (personal communication). At no time during our passages at sea or on any of the islands visited in the winter of 1950 did we see adult males except as single individuals.

It seems probable that the adult males leave the vicinity of the San Benitos after the breeding season. That they may migrate northward as far as California seems possible. A very high proportion of adult males has been observed in non-breeding aggregations in that state. Thus on April 22, 1950, Bartholomew estimated that fully 80 per cent of the 956 sea lions on a sandy beach on San Nicolas Island were adult males. On July 9, 1949, there were on this same beach 164 sea lions, nearly all males. The overwintering population of sea lions on a beach in Monterey County south of Point Sur, with numbers estimated by Hubbs as high as 1800 and by others still higher, consists largely of adult males of this species, with

TABLE 1.—*Pinniped populations in January and February, 1950, on certain islands off the northern coast of Baja California*

DATE	PLACE	ZALOPHUS	MIROUNGA
Jan. 27–Feb. 3	Guadalupe	165	4,548
Feb. 4–7	San Benitos		
	East Island	4,069	550
	Middle Island	3,438	175
	West Island	2,207	183
	San Benito Totals	9,714	908
Feb. 7	Cedros	340	0
Total		10,219	5,456

a few Steller sea lions. Fry (1939) has indicated the possibility of a winter movement of sea lions into California from Baja California.

Mirounga angustirostris (Gill). Northern elephant seal.—Prior to their commercial exploitation, elephant seals occurred in large numbers on the San Benitos, and these islands were perhaps the first outside of Guadalupe to be reoccupied by breeding colonies of this species as its numbers increased. Individuals and small groups have apparently been hauling out on these islands for many years. Hanna (1925) reported that at least six were seen in the islands as early as 1918. According to Williams (1941) the animals probably established themselves first on East Island.

At least since 1925 (Bancroft, 1932) the elephant seal has been present on the San Benitos in some numbers, although the size of the total population on all these islands apparently had never been determined prior to our visit. In August, 1946, Hubbs saw at least five dead and at least three live bulls on the north shore of West Island, and at least eleven live cows and bulls on the west side of Middle Island. In March, 1948, there were elephant seals on all three islands and "at West San Benito Island approximately 700 elephant seals were indicated by shore counts" (Fitch and Wilson, 1949). On July 29, 1949, J. L. McHugh (personal communication), on the basis of rather thorough observations, estimated the elephant seal population on Middle Island as 500. On February 4–7, 1950, we found 183 elephant seals on West Island, 175 on Middle Island, and 550 on East Island, bringing the total for the San Benitos to a minimum figure of 908 (Table 1).

Elephant seals of both sexes and all ages were present at the time of our visit and breeding activities were being carried on with great vigor and enthusiasm on each of the islands.

CEDROS ISLAND

We did not completely circumnavigate Cedros Island, but on February 7 and 13, we cruised along the whole length of the east coast of the island close inshore. As the sea was calm and the visibility was excellent, we were able to examine the entire stretch of coast in detail. Despite mile after mile of beautiful smooth beach not a single elephant seal was seen and, aside from three California sea lions seen off Cedros Village on February 7, and 12 sea lions observed off the southern end of the island on February 13, no pinnipeds of any kind were seen except in a cove south of the North Lighthouse. Here, on February 7, we counted on the sandy beach 340 sea lions, including not more than fifteen adult males.

SUMMARY

In the last week of January and the first two weeks of February, 1950, on a trip to Guadalupe, San Benito, and Cedros islands, Baja California, aboard the Research Ship *Orca*, the authors made a census of the pinnipeds on each island. A careful, but completely unsuccessful, search was made for a possible remnant population of the Guadalupe fur seal.

On Guadalupe the population of the California sea lion, although larger than previously reported, still was very small, numbering well under 200, and it did not appear to be expanding. The rapidly growing elephant seal population was found to contain more than 4500 individuals. Since there is every indication that the population is still on the steep part of its growth curve, it is predicted that the numbers of this species will continue to increase greatly.

On the San Benitos both California sea lions and elephant seals were extremely abundant (9714 and 908, respectively) and the breeding activities of the elephant seals and the population structure of the sea lions suggested that the populations of both were still expanding.

We examined only the east side of Cedros Island and found no pinnipeds ashore except a herd of 340 California sea lions near North Lighthouse.

Adult male sea lions were conspicuously absent both at sea and on the islands visited. There is some indication that the adult males may move to California after the breeding season.

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ADDITIONAL NOTES ON FOSSIL AND SUBFOSSIL BATS FROM JAMAICA

BY ERNEST E. WILLIAMS

Very recently (Koopman and Williams, 1951) fossil bats collected by H. E. Anthony in 1920 in caves in Jamaica have been described. One new species and two other forms new to Jamaica were cited.

During the summer of 1950 the writer, Karl F. Koopman, and Max K. and Bessie M. Hecht visited Jamaica with (in part) the objective of visiting the more important cave localities examined for fossils by Anthony, verifying the nature and condition of the fossiliferous deposits *in situ* and collecting cave fossils to the extent possible. In Anthony's best localities it proved no longer possible to secure additional specimens of the more ancient layers he had collected, but new fossils were nevertheless obtained, apparently intermediate in age between the Recent fauna and that of Anthony's older layers.

The fossil lizard material secured by the 1950 group, as well as that collected by H. E. Anthony on the earlier expedition, is under study by Max K. Hecht and will be reported by him. The fossil bats of 1950 are here recorded.

The closeness in age and relationships of the known cave fossil faunas to that of Recent time has made essential an on the spot acquaintance with the Recent fauna. The 1950 expedition had as an important objective the collection of the Recent fauna (both inside and outside caves), including living bats and bat skulls in owl pellets. This Recent material assists importantly in the interpretation of the fossils.

Strata and faunas.—The fossil Jamaican bats reported in Koopman and Williams (1951) were found in layers thought to be of considerable but indefinite age (perhaps Pleistocene), and characterized by the presence of abundant remains of a giant representative of the lizard genus *Celestus*. These strata have consequently been called "lizard layers." In terms of bat faunas these layers are distinguished by the fact that they contain only forms now extinct or relatively scarce in Jamaica. In particular they contain an extinct endemic species of the phyllostomatine bat genus *Tonatia*—*Tonatia saurophila* related to *T. bidens* of the mainland.

No additional material from these layers was obtained during the 1950 expedition, but in Portland Cave, Clarendon Parish, and in Dairy Cave, St. Ann Parish, collections were made in fossiliferous layers apparently closer to the Recent in

TABLE 1.—*Fauna of the Lizard and Bat Layers*

LIZARD LAYERS		BAT LAYERS			
		Dairy 1950			
Wallingford	Dairy 1920	West Side		East Side	Portland
		Upper Level	Lower Level		
Tonatia	*Tonatia*	—	—	—	—
—	—	*Macrotus*	—	*Macrotus*	*Macrotus*
—	*Brachyphylla*	—	—	—	*Brachyphylla*
—	*Ariteus*	—	—	*Ariteus*	—
Reithronycteris	*Reithronycteris*	—	—	—	*Reithronycteris*
—	—	*Erophylla*	*Erophylla*	—	*Erophylla*
—	*Mormoops*	*Mormoops*	—	—	—
—	—	*Chilonycteris*	*Chilonycteris*		*Chilonycteris*
Natalus	—	—	—	—	—
Eptesicus	—	—	—	—	—
—	—	—	—	—	*Monophyllus*

age. These layers did, indeed, contain lizards, but their most abundant vertebrate components were bats. They are, therefore, called "bat layers."

In the bat layers *Tonatia* does not occur, and the subfamily is represented by the still living and very common *Macrotus waterhousei* (unknown in the lizard layers). *Chilonycteris parnelli* becomes a characteristic and numerous constituent of the fauna. In one area (Portland Cave) *Brachyphylla*, one of the genera of the lizard layers now extinct in Jamaica, lingers into the fauna of these strata, but *Artibeus jamaicensis*, the commonest bat of the Recent period (both living and in Recent owl pellets) is quite unrepresented. In every aspect these layers seem to present us with a transition fauna.

Table 1 lists in parallel columns the faunas of the lizard layers (listing the two localities for these layers separately) and of the bat layers (two caves and four collections).

The inferred intermediate position in time of the bat layers cannot, unfortunately, be confirmed by actual stratigraphic sequence in either of the caves in which bat layers are known.

In Portland Cave the deposit containing the bats was found at the left of the entrance 18 to 20 inches below the original surface from the side of an excavation for phosphate. There were remnants of a kitchen midden including some marine shells at the surface. The zone chosen for collection was rich in land shells and bones, but was of very limited extent, only about a foot in length horizontally. Though the phosphate excavation was five to six feet deep over a considerable area no indication was found of bone-containing layers deeper than the one collected or in fact at any other level. There is reason to believe that the pocket of bones constituting the bat layer were the accumulated pellets of an ancient owl. Portland Cave fronts on the sea and was presumably formed by marine action. Its floor is red cave earth which is for the most part dry and powdery. Bats now inhabit the cave, but no owls, and there is no surface accumulation of bat skulls.

There can be distinguished in this cave only the surface and subsurface layers (the latter, so far as the 1950 expedition could determine, contained no bats or *Oryzomys* and only rather rarely *Geocapromys browni*) and the single bone pocket which represents the bat layer.

The other cave from which bat layers come is one in which Anthony did obtain a considerable sample of the lizard layer and for which he described the remaining portions of that layer as containing millions of bones. The area which he worked (described in his notes as being 50–100 yards west of the entrance) is now buried under a broken rock floor, the Jamaican government having completely transformed the portion of this cave near the entrance in an attempt to provide a place for rum storage during the second World War. The 1950 party was, therefore, compelled to search deeper in the cave. Four collections were made, one without mammals, the other three recorded in Table 1.

Of the latter, two collections from the west side of the cave were very similar, recovered from rather moist dark brown earth between levels of a dripstone floor, the collection from the upper level being richer in bones, the collection from the lower level, separated by a ledge of dripstone, being much the poorer. The depth of these layers underneath the original cave floor was impossible to determine. A good portion of the original floor had been removed, and all of it was very uneven in this portion of the cave. The bones here obtained were heavily encrusted, not with limestone, but with some apparently nitrogenous material.

The single productive collection from the east side of Dairy Cave came from a dry gravelly deposit about two feet underneath a dripstone floor. Dairy Cave again fronts on the sea and was probably marine in first formation, but it has many chimneys to the outside and much dripstone formation in spite of now being very dry. It has evidently passed through alternate wet and dry periods. The bat layers were in each case at least 50 yards further from any entrance or opening than were Anthony's lizard layers.

The author thinks the evidence of the included faunas is adequate demonstration of the intermediate temporal position of the bat layers. Certain genera do appear to be valid markers of faunal change and temporal succession. Thus, the presence of *Artibeus*, now the commonest Jamaican cave bat, marks the most

Recent period and the most superficial layers (indeed according to some evidence to be mentioned later, its dominance may be quite recent). *Tonatia*, on the other hand, is an indicator of the oldest Jamaican bat faunas of which we have any knowledge. *Macrotus* and *Chilonycteris* with *Brachyphylla* or *Ariteus*, and in the absence of *Artibeus*, show us a transition fauna very close to the Recent.

The nature of the deposits.—The Jamaican deposits containing fossil bats and lizards are probably in all cases ancient owl pellet deposits. This was Anthony's own conception of the lizard layers (as recorded in his field journal), and it is a view considerably reinforced by the collections, made during the 1950 expedition, of a number of owl deposits, some in the process of formation and some older, which show the type of material which was very probably the precursor of the fossiliferous formations.

Collections made at two localities are important: (1) *Ferry Cave between Kingston and Spanishtown*. Remains from owl pellets were here collected in a cave in which the owl still lived. Pellets were collected in various stages of disintegration, on the surface and from little pockets in irregularities of the cave floor. (2) *A rock ledge at Antrim, St. Ann Parish*. Here a bone deposit two to six inches deep and covering a ledge and crevice area of several square feet testified to the work of perhaps generations of owls. The bones seemed for the most part not as fresh as at Ferry Cave, though they were not so old that all traces of matted hair and other organic material had rotted away. This deposit is being studied by K. F. Koopman. The discovery of the second complete skull of *Reithronycteris aphylla* Miller in this deposit has been discussed by him in a paper in this Journal (Koopman 1952, p. 256). A preliminary account of its other mammalian fauna is included.

From the bones of the rock ledge at Antrim to the bat layers of Dairy Cave only a few miles away is a small step topographically and also in the character and quality of the remains and the included fauna. Similarly it is an easy transition from the bat layers of Dairy to the bat layers of Portland Cave. The latter differ very little except in some of the included fossils from the lizard layers of Dairy Cave. These again are faunal and lithologic transition stages to the lizard layers of Wallingford Cave.

Apart from this series which connects known owl deposits with the fossiliferous strata, the overall content of the bat-containing layers is itself evidence for owl pellet origin. Lizards, birds, and mammals of generally small size are characteristic of these layers. The largest mammal found in these deposits is *Geocapromys browni*, and a very large proportion of the bones of this animal are those of young individuals. The largest lizard is the giant *Celestus* of the lizard layers, some individuals of which must have been well over two feet long, probably too big for owls of Recent type to take. In this case, it is possible that the layers which contain this form do not record the total range in time of a giant *Celestus* (the fossil may be identical with or ancestral to *C. occiduus* Shaw, a few individuals of which were collected as late as the early 19th century); instead they may record the range in time of an extinct giant owl capable of carrying these large lizards. It is known that a giant owl did exist in earlier times in Hispaniola (Wetmore,

1922); it is by no means unreasonable to believe that an owl similar or larger once existed in Jamaica.

It should be kept in mind that terrestrial deposits quite different from those which contain bats and lizards are known in Jamaica. The hard breccias, for example, are such deposits (Anthony, 1920 *a* and *b*, Koopman and Williams, 1951). In these the pond turtle (*Pseudemys*) and *Crocodylus* as well as the giant rodents described by Anthony (1920*a*) are found. A pond turtle and a crocodile imply an aquatic character for the fauna, and perhaps the rodents fit this picture also. It is probable that the hard breccias of Wallingford Cave, St. Elizabeth Parish, and the mixed breccias of Sheep Pen Cave near Windsor, Trelawney Parish, are flood deposits or reworked flood deposits. Both caves are near substantial streams,

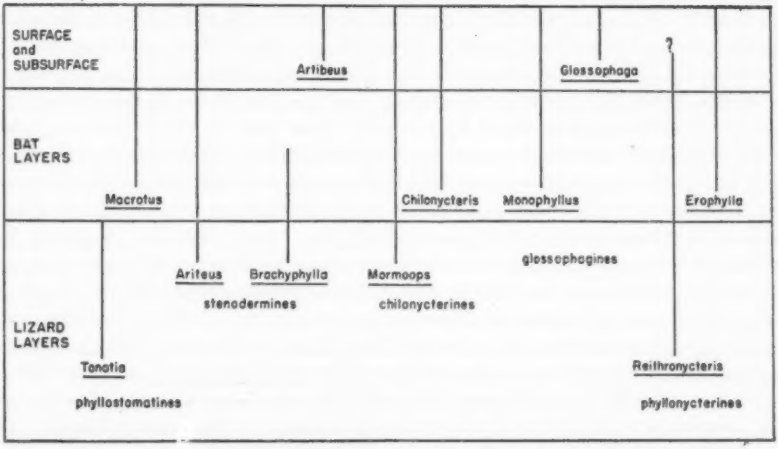

FIG. 1.—Inferred temporal range of certain Jamaican bats; Phyllostomatidae.

and the whole character of these caves is very different from that of such sea-fronting caves as Portland or Dairy. It is possible that similar deposits should be looked for in other caves along the course of major streams in Jamaica.

Long Mile Cave near Windsor, Trelawney, exhibits another deposit which is not likely to be of the same origin as the typical bat-containing strata. Here *Geocapromys* and a monkey are the only mammals definitely recorded. Giant *Celestus* does occur, and this fact was the reason for the assignment of the deeper strata of this cave to the "lizard layers" in Koopman and Williams (1951). Some portion of the bone remains in this cave may be owl-derived, but not a major portion. The situation is confused by the fact that a kitchen midden of post-Columbian age occupied the surface of the cave floor, and in the thirty years since Anthony made the collection here the midden material has apparently become commingled with the deeper material. There is no stream nearby at present, but the large size of many of the bones from this cave makes it seem possible that the deeper layers here may be flood or fissure deposits.

It is worth recording that C. Bernard Lewis of the Jamaica Institute has found *Geocapromys* in the upper levels of the banks of one of the streams near Kingston. The genus is unknown in that area today. There is hope, therefore, that Pleistocene or even Tertiary remains of land vertebrates may be found in the stream beds of Jamaica. All such flood deposits will, of course, be quite different in content and character from the bat-containing strata which have been principally under discussion. Investigations of these two sorts of deposit will certainly be for a long time independent of one another. Each offers good prospect of interesting discovery, but it will be a long time before they can be correlated with one another except with serious difficulty.

Problems of faunal change.—In Fig. 1 the most probable vertical range of the phyllostomatid bats found fossil in Jamaica has been diagrammed. No accurate time scale can be suggested, and length of line in the diagram is not to be interpreted in terms of any definite measure of elapsed time. Only probable succession is indicated. In some respects even this is quite hypothetical. Thus, *Tonatia* is shown as present in Jamaica at an earlier time than *Brachyphylla* on the hypothesis that the Wallingford lizard layer is older than that of Dairy Cave, a judgment supported only by the presence in Wallingford of a fossil species of *Natalus* not known in any other deposit. It hardly needs emphasis that with the very small samples available the significance of the presence or absence of one genus cannot be established. Some of the details of Fig. 1 may, therefore, justifiably be regarded with scepticism, though on present evidence they are at least as plausible as any alternative. On the other hand, other points stressed by the diagram, the replacement of *Tonatia* by *Macrotus* or the lateness of arrival in Jamaica of *Artibeus* may be regarded as well established; these points are so well checked by a number of cross correlations that there can be very little reason to doubt them.

An important feature of faunal change as we begin to know it in the bat faunas of Jamaica is replacement of one genus by another of the same subfamily. In the 1951 paper it was tentatively suggested that this phenomenon should be looked for in all of the subfamilies of Jamaican bats and was to be looked for as a phenomenon probably still occurring. It must be admitted that for the majority of the Jamaican subfamilies the present evidence is quite inadequate to indicate or disprove replacement or tendency to replacement. For a few groups the evidence is highly interesting and suggestive. The stenodermines are one such group. In this subfamily there is some indication of a reversal of dominance of two forms in post-Columbian times.

The known history of the Stenoderminae in Jamaica begins with *Ariteus* and *Brachyphylla* present together in the Dairy fauna of lizard layer age. The competitive relation, if any, between these genera at that time is beyond our knowledge. *Ariteus*, however, survives to the present time. *Brachyphylla* is now unknown in Jamaica. In at least one area—the arid peninsula, probably at that time an island, of Portland Ridge—*Brachyphylla* did, indeed, survive during part at least of the age of the transition faunas. *Ariteus*, so far as we know, did not share this area with *Brachyphylla* (though it occurred there later according to the evidence of subsurface skulls collected by Anthony in 1920).

In Dairy Cave, in collections interpreted as being of transition (bat layer) age, and possibly contemporaneous with the Portland Ridge fauna, *Ariteus* occurs without *Brachyphylla*. Perhaps *Brachyphylla* was for a time restricted to the Portland Ridge island, while *Ariteus* had displaced it on the Jamaican mainland. Perhaps somewhat later (in the period during which the subsurface layers were being laid down) *Ariteus* displaced *Brachyphylla* even on its Portland Ridge refuge. Still later (as collections of Recent bats show) *Artibeus* wholly or principally replaced *Ariteus* on Portland Ridge.

Whether or not the history of stenodermines on Portland Ridge had quite the simple pattern here suggested, there is abundant evidence in subsurface collections from a number of mainland caves that *Ariteus* was at one time a very common bat. In subsurface time *Artibeus* was always less common than *Ariteus*, although it was often commoner than any bat genus except *Ariteus*.

The period during which *Ariteus* was commoner than *Artibeus* extended from pre-Columbian time (subsurface deposits without *Rattus* and sometimes with *Oryzomys*) to early post-Columbian time (older surface deposits containing *Rattus*).

The bone deposit at Antrim is one of the later deposits in which *Ariteus* is common. In it the relation between the two genera in terms of fragments preserved is about three or more *Ariteus* to one *Artibeus* (20 skulls, 7 rostra, 35 complete mandibles, and 56 part mandibles of *Ariteus* as compared with 6 skulls, one rostrum, 14 complete mandibles, and 8 part mandibles of *Artibeus*). This abundance of *Ariteus* in the older surface and in the subsurface owl deposits is in striking contrast to its scarcity in museum collections and in the experience of collectors of the present day bat fauna. It is certain that *Ariteus* is a living form. The Jamaica Institute has six specimens of the genus collected in or around Kingston since 1940. It was not obtained alive by Anthony in 1920 on the mainland or on the Portland Ridge peninsula or by other professional collectors since then. It was not found by the 1950 party as a living animal, although living *Artibeus* was present in almost every bat-inhabited cave. The scarcity of *Ariteus* in modern collections may nevertheless be an artifact of collecting methods; *Ariteus* may not be a cave bat, and its habitat might be unknown to collectors. Here the evidence of Ferry Cave is important.

In Ferry Cave the most recent owl pellets containing bats were collected. (Other very recent owl pellets contained only *Rattus*.) The owl which was the source of the pellets was seen in the cave. Some of the pellets were incompletely disintegrated. Here the proportion of *Artibeus* to *Ariteus* in the collection was reversed—there were 42 skulls of *Artibeus* to five of *Ariteus*. It thus appears that predatory owls at present find *Ariteus* relatively scarce just as do human collectors. A real shift in the relative abundance of *Ariteus* and *Artibeus* in historical time appears probable.

A possible explanation of such a shift may be suggested. The stenodermines are frugivorous. *Ariteus* is the endemic, *Artibeus* the continental form. As was impressively evident to the 1950 party during a trip which extended over the greater part of Jamaica, the endemic vegetation of great areas of that island has

been mostly destroyed and replaced by exotic types. Many, or in some areas most, of the trees were imported species. It is easy to see that for frugivorous forms such changes in the flora might be important as implying radical changes in the available food. Or, if food were not critical, if one of our two competing forms were not cave but tree dwelling, the disappearance of the native forest may have eliminated or reduced the preferred habitat. In regard to either factor it is probable that the wide ranging continental form would be less narrowly adapted than the island endemic.

That the change in the relative frequency of *Ariteus* and *Artibeus* has occurred in post-Columbian time is, on the hypothesis of the importance of change of floras, not at all surprising. It is certain that human modification and human occupancy of the Jamaican area have proceeded at an ever accelerating pace since the Columbian discovery. It is possible that the change in the abundance of the two genera dates from some specific agricultural change.

The *Tonatia-Macrotus* succession in Jamaica is not quite as well documented as the stenodermine sequence; the date of the shift and the reasons for it can only be guessed at at present. Both forms are insectivorous. The most conspicuous difference in morphology is that one form is relatively short-faced (*Tonatia*), the other relatively long-faced (*Macrotus*). We lack any adequate knowledge of the ecologies of these forms and equally any knowledge of the temperature and humidity changes which may have had their influence at the time (possibly Pleistocene) when the replacement of one form by the other occurred. The present distribution of the two genera is perhaps a clue to a difference in climatic preferences. *Tonatia* extends from tropical South America north to British Honduras, *Macrotus* from the southwestern United States south to Guatemala. According to Goodwin (1942), the two genera perhaps both occur in Honduras.

It is probable, judging from this distribution, that *Tonatia* is the warmer climate form, *Macrotus* a form of relatively cooler climates. It is possible, therefore, that *Tonatia* was present on Jamaica during the last interglacial, and that *Macrotus* replaced it during the cooler climates of the last glacial period. It may be supposed that since that time either the climate of Jamaica has not returned to that degree of warmth most favorable to *Tonatia* or that for other reasons *Tonatia* has not been able to reinvade.

Rather similar changes in the frequency of genera during the period recorded by the available series of deposits are suggested by the present evidence for the other subfamilies and families of Jamaican bats, but that evidence is so meager that it is not to be relied upon. No suggestions can now profitably be made as to the reasons for such apparent frequency changes.

Enough has now been said to indicate that the bat-containing deposits in Jamaica offer interesting examples and problems of faunal change. The results secured from the relatively few collections that have so far been made promise richer rewards from fuller study.

A partial series has so far been assembled of deposits extending backward in time from those still being formed through a number of intermediates to some that may well belong within the last Pleistocene glaciation. This series, if properly

supplemented and completed, may give us a relatively sensitive picture of the successive faunistic and ecological changes in a certain portion of the animal population of Jamaica, that portion which was eaten by owls. The picture so obtained will, of course, be a limited one. Its interest will lie in its probable relative completeness for the types of animals represented. These owl-deposited remains will not yield any animals as large or spectacular as the giant rodents of the hard breccias (or those animals which may be present in Tertiary flood deposits if they can be discovered). But, because the sequence of forms may be much closer and more clearly seen than any which seem in prospect in other deposits in Jamaica, they may be very valuable in the understanding of one important segment of Evolution—the succession of faunas in time and the concomitant problems of competition and extinction. The special features which the study of these problems on an archipelago will add will not lessen their interest.

Acknowledgments.—Thanks are due to Dr. H. E. Anthony for the privilege of consulting his field notes for the 1919–1920 Jamaican expedition and for opening the facilities of the Department of Mammalogy of the American Museum of Natural History to the study of the 1950 collections, to Mr. C. B. Lewis of the Jamaica Institute for many courtesies and a great deal of personal assistance during the stay in Jamaica, to Mr. J. Lewis for his help in the important discovery of the Antrim deposit, to Dr. A. S. Romer for making possible the 1950 expedition and for critically reading the manuscript, to Miss Barbara Lawrence for the privilege of the use of the mammal collections of the Museum of Comparative Zoology, Harvard College, to Dr. Karl F. Koopman for making the careful comparisons required for the final identification of the fossil material and for his important contributions in Jamaica, and to Mr. Max K. Hecht and Mrs. Bessie M. Hecht for whole-hearted participation in the collection of mammalian fossils as in all other phases of the Jamaican expedition.

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OBSERVATIONS ON LEMMINGS FROM BARTER ISLAND, ALASKA

By Robert L. Strecker and Peter R. Morrison

Although lemmings are the most abundant and perhaps the most characteristic of Arctic mammals, there is little published information on details of their life history. Degerbøl and Møhl-Hansen (1943) describe reproduction and moult in captive *Dicrostonyx* from Greenland, Sutton and Hamilton (1932) and Shelford (1943) give information on the numbers and appearance of lemmings in the Hudson Bay region, and Rausch (1950) discusses the ecology and abundance of lemmings (chiefly *Lemmus*) in the vicinity of Barrow, Alaska. Included here are some further observations on the midsummer habitat of the lemmings on the Arctic slope, and data on the growth of young collared lemmings (*Dicrostonyx rubricatus rubricatus*) in captivity.

Observations in the field were made along the Arctic Ocean at Barter Island, Alaska (lat. 70°, long. 144°), and the adjacent mainland from August 9 to 14, 1950. Subsequent studies on the animals in captivity were made at Fairbanks, Alaska (August 15 to September 5) and at Madison, Wisconsin (September 6 to January 6). These observations were made incidental to a study of temperature regulation in mammals supported in part by contract with the Air Materiel Command, U. S. Air Force, and research grant from the Wisconsin Alumni Research Foundation. We are particularly indebted to the Arctic Aeromedical Laboratory, Ladd Air Force Base, for its facilities and assistance which were extended through Col. J. Bollerud. The identification of the specimens is through the kindness of Dr. H. W. Setzer and Dr. D. H. Johnson of the U. S. National Museum.

The tundra at and near Barter Island is superficially quite flat although in many areas there are numerous depressions and ridges one to four feet in height, attributed to freezing and heaving of the ground. The ground cover at this time was a mat of grasses and sedges, with numerous small wild flowers and occasionally scrub willow from several inches to a foot high. There was an abundance of tunnels and open runways along these ridges and out onto the adjacent flat areas. Although droppings were common and appeared fairly fresh, evidently due to the preserving action of the cold wet weather, the lemmings themselves were very scarce, as was also noted in the Point Barrow region during the summer of 1950 by Daniel Q. Thompson. Over a four-day period of intensive search, 30 "Sherman" live traps with solid or mesh top and sides were kept set and baited and several hundred tunnels were dug up. Only two brown lemmings (*Lemmus trimucronatus alascensis*) and three collared lemmings (*Dicrostonyx r. rubricatus*, one with young) were taken. Of these animals, three were captured by hand after observation, two were dug out of tunnels (one with young), and one was taken in a trap. Once an active runway had been discovered, the darker and moister fresh droppings could readily be distinguished from very common old droppings. Most of the tunnels were quite short, averaging about a foot in length. The ground was nearly saturated and the tunnels, usually only two or three inches from the surface, were cold and damp. There would commonly be an open runway through the grass, and every four or five feet a short tunnel with a single opening. Appar-

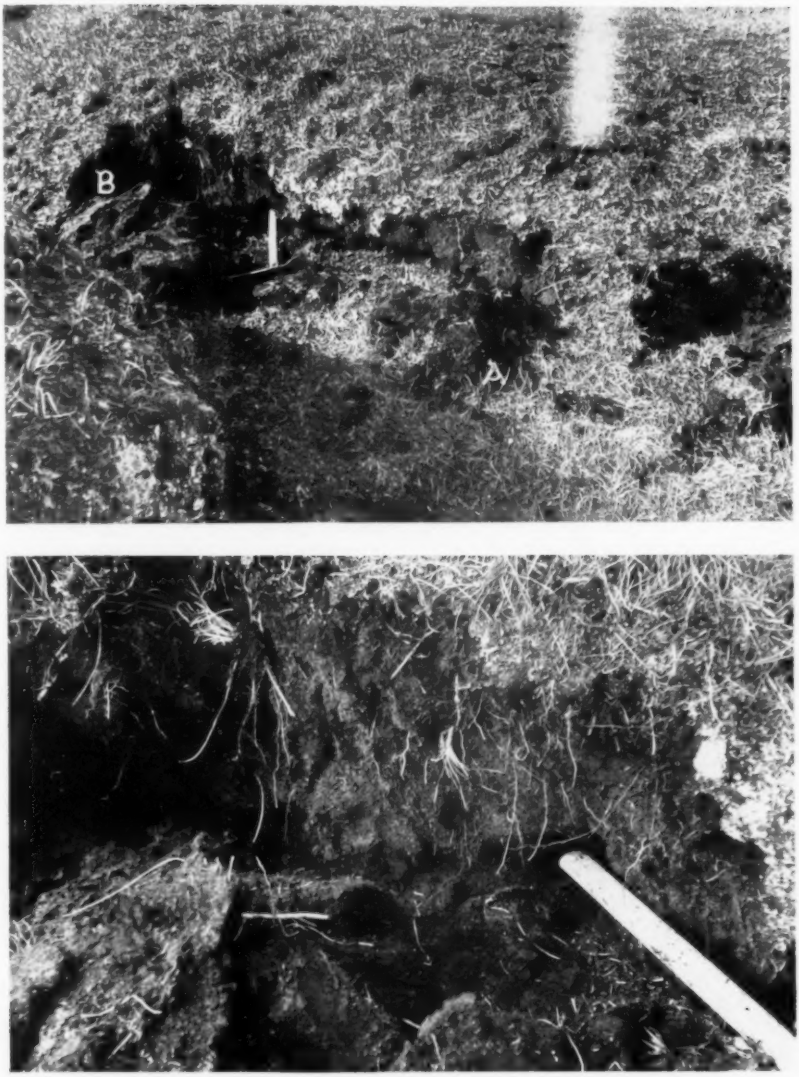

PLATE I

The excavated tunnel in which the litter of collared lemmings was found. The upper figure shows the entire tunnel, with the entrance at A, the nest cavity at the tip of the pick handle, and the termination of the burrow at B. The lower figure is a close-up view of the nest cavity and adjacent tunnel.

ently the lemmings forage out along these runways, using the tunnels for temporary shelters. The runways were very distinct although never worn bare. Preble (1902) reported that lemmings in the Hudson Bay region did not form runways.

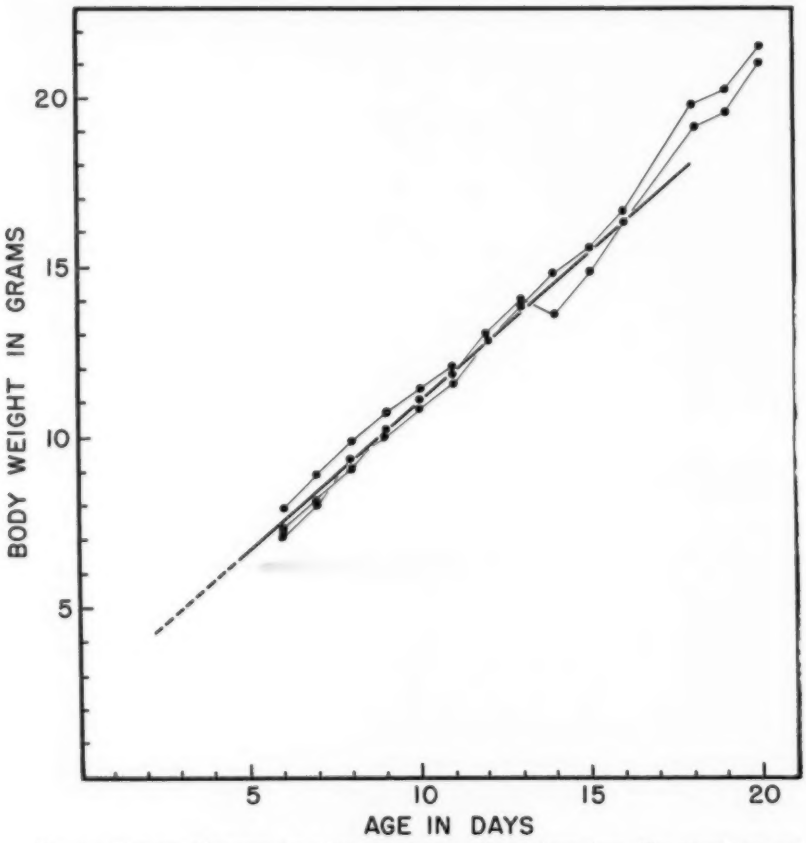

FIG. 1.—The growth curve for a litter of young collared lemmings. The "true" age of this field caught litter was estimated from the date the eyes opened, following the observation of Kolthoff (1903).

All of the specimens, with the exceptions of the moribund, trap-caught brown lemming, were held in small cages (6″ x 6″ x 12″) with abundant natural nesting material. They were first supplied with various indigenous herbaceous plants, and later with fresh vegetables, of which carrots were the preferred item. The animals were never observed to drink water although it was always furnished. This is in accord with the observations of Degerbøl and Møhl-Hansen (1943) who routinely

maintained their animals without water. Details of their preference for a variety of non-indigenous food stuffs is compared with that of several other Alaskan mammals elsewhere (Tietz and Morrison, in preparation). The animals appeared to thrive in captivity, and it is felt that losses sustained were the result of rigorous experimental conditions to which they were occasionally subjected. The brown lemming was difficult to handle, indeed behaving in many respects, as in appearance, like a large meadow vole. One of the collared lemmings was difficult to handle, but the others were very docile from the start. In this, their behavior was very similar to the hamster, which they also resemble in general appearance.

Of particular interest was the discovery of a litter of four young with one of the collared lemmings. The tunnel in which the nest was located ran parallel to the base of a depression about three feet deep. The tunnel was from 4 to 8 inches back

TABLE 1.—*Growth and weight maintenance of two collared lemmings in captivity*

DATE	NO 2 (GRAMS)	NO 6 (GRAMS)
Aug. 15		54.2
Aug. 16	23.1	
Aug. 17	23.1	
Aug. 28	28.1	46.7
Aug. 30	30.2	43.8
Sept. 2	28.4	
Nov. 28	37.5	
Nov. 30		43.0
Dec. 5	38.5	
Dec. 7		47.5
Dec. 12	37.0	
Dec. 14		41.0
Jan. 30		50.0
Feb. 2		49.0

in from the bank surface, was in all about 9 feet long, and had only one entrance (Pl. I, upper). It varied from 2 to 3 inches in diameter, and had along it six small side chambers about two inches in diameter, several of which contained mounds of droppings. The nest chamber itself was a rounded expansion of the tunnel four inches in diameter, filled with grass cut in about one-inch lengths. Although the rest of the tunnel was quite damp, the nesting material was dry. The four young were in the nest, which was about six feet from the entrance of the burrow. The mother was found at the very end of the tunnel, three feet further on. In captivity, the mother did not object to our handling of the young although if one were placed outside the nest she would immediately carry it back. During the four-hour trip, from Barter Island to Fairbanks, she killed and partly ate one of the young, but this behavior was probably brought on by the disturbance of the flight.

Kolthoff (1903), cited by Degerbøl and Møhl-Hansen, reported that the eyes of the young open at about 14 days. By this criterion our litter was six days old

on discovery. The family was caged and fed as were the others. During the following several weeks they were weighed and examined daily. Descriptive data on the four young was as follows:

August 15 (*ca.* 7 days).—The young, two males and two females, were well furred dorsally with tan hair, and with a conspicuous dark streak down their backs. Ventrally the hair was fine and cream colored. The eyes and external ears were closed. The incisors were visible, but not yet through the tissue of the jaws. The mammae were plainly visible as tiny dark dots on the females.

August 16 (*ca.* 8 days).—The dorsal fur appeared quite lustrous. The incisors had broken through the jaw tissue.

August 18 (*ca.* 10 days).—One female killed by mother. Well furred all over. Sleep in an upright sitting position.

August 19 (*ca.* 11 days).—Becoming quite active, moving around cage. Mammae still visible on female, but becoming less so due to growth of fur.

August 22 (*ca.* 14 days). The eyes opened, and the animals were quite active. One male died.

The growth of the young lemmings during the first three weeks is shown in Figure 1. During this period the average growth curve closely follows a straight line with a slope of 0.89 gm./day. Such linear curves have also been observed in *Clethrionomys* from Alaska and *Peromyscus* from Wisconsin (unpublished observations), with growth rates, as here, of slightly less than 2 per cent of the adult weight per day.

The weight maintenance of two of the captured collared lemmings over a six-month period in captivity is shown in Table 1. Lemming No. 6, the mother of the litter, lost almost 20 per cent of her weight during the first two weeks, but this was largely regained. No. 2 gained 70 per cent in weight during the succeeding four months. The third collared lemming weighed 17.1 grams following capture, but lost weight and died after three days of intensive study, involving cold stress.

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SHREW PREDATION AND VOLE POPULATIONS ON A LOCALIZED AREA

By W. Robert Eadie

Observations on the predatory relationships of short-tailed shrews (*Blarina brevicauda*) to meadow voles (*Microtus pennsylvanicus*) were made at various intervals over a period of seven years on the same area in the vicinity of Ithaca, New York. The study area covered about 150 acres of non-cultivated unused fields broken by hedgerows into smaller units of 5 to 20 acres. Most of these were covered with a vigorous growth of various grasses, weeds, and briar clumps with occasional invading shrubs or young trees. Several more recently cultivated fields had a persistent uniform covering of timothy (*Phleum pratense*).

The reality of shrew-mouse predation has been established by a number of observers. A brief review of the literature and further evidence of such predation from these study areas has previously been presented for a year of high, and a year of low, vole abundance, 1942–43 and 1943–44 (Eadie, 1944; 1948). Some of the data from these reports are incorporated here with additional data from five other years from 1946 to 1951. It was not possible to observe the areas during 1944 and 1945.

The special features of a predator-prey relationship between such diminutive mammals are not grossly apparent or easily observable. The small size of the participants and their secretive habits under cover of ground vegetation lends a high degree of obscurity to their activities. The evidence available, therefore, is partly indirect, circumstantial, and incomplete, but does give us some clues to the possible relationships between these mammals. The evidence of actual predation is gleaned from the analysis of food remains in *Blarina* scats from the fall and winter months, and from data gathered at winter nesting quarters of the shrews. In addition, quadrat studies in the areas yield data which indicate relative population trends from year to year that may have some significance.

Food studies.—*Blarina* scats were mostly collected in the early spring from midden heaps near nests and runways. These were accumulations from the preceding fall and winter and showed varying degrees of weathering dependent upon the amount of overlying cover at the site. During one fall and winter, monthly collections were made from runways by a technique described previously (Eadie, 1948). In Table 1, vole remains in the scats are reported by frequency percentage for those years when such information was obtained. The figures for 1945–46 and 1950–51 were obtained by taking random samples from a mass of droppings that were amalgamated by weathering.

It may be seen that vole remains appear consistently in the scats of the short-tailed shrew in every year studied. The frequency percentage of occurrence is fairly uniform for the various years with the outstanding exception of 1942–43 when *Microtus* numbers were at an extreme high on the area and 56 per cent of the shrew scats contained vole remains.

Relative population trends.—Quadrat studies on these same areas yield data on relative population trends of *Blarina* and *Microtus* from year to year. These

quadrats were uniformly of quarter-acre size placed in favorable *Microtus* habitat. The relative population figures obtained represent initial 24-hour catches from a uniform number of approximately 60 snap traps set in grid fashion over each quadrat. Results obtained during extremes of weather conditions were excluded. Fall quadrats only, when local small mammal populations are at their yearly peak of abundance, are considered here (with the exception of 1950–51,

TABLE 1.—*Frequency percentage of Microtus remains in fall and winter scats of Blarina for 5 separate years. Figures for 1945–46 and 1950–51 represent random samples from a fused mass of droppings*

FALL AND WINTER PERIOD	NO. OF SCATS OR SAMPLES	FREQUENCY PERCENTAGE	MICROTUS POPULATION LEVEL (FALL)
1942–43	200	56	High
1943–44	255	14	Low
1945–46	103	16.5	No data
1946–47	67	18	Moderately high
1950–51	194	14	Low

TABLE 2.—*Number of Microtus and Blarina trapped from one-quarter acre quadrats in initial 24-hour periods, 1942–43 and 1948–51*

DATE	MICROTUS	BLARINA	DATE	MICROTUS	BLARINA
Oct. 6, '42	20	2	Sept. 13, '49	9	4
Nov. 20, '42	20	0	Sept. 15, '49	2	4
Ave. 1942	*20*	*1*	Sept. 23, '49	4	5
Aug. 11, '43	2	2	Oct. 5, '49	5	4
Sept. 29, '43	9	3	Oct. 7, '49	9	4
Oct. 31, '43	10	0	*Ave. 1949*	*5.8*	*4.2*
Dec. 10, '43	9	3	Apr. 19, '50	0	2
Ave. 1943	*7.5*	*2*	Aug. 4, '50	0	3
Aug. 21, '46	16	2	Aug. 7, '50	0	1
Aug. 19, '47	4	4	Aug. 14, '50	3	2
Oct. 1, '47	6	3	*Ave. 1950 Fall*	*1*	*2*
Ave. 1947	*5*	*3.5*	Apr. 20, '51	0	2
Aug. 10, '48	9	2	Apr. 24, '51	0	1
Oct. 8, '48	3	9	*Ave. 1951 Spring*	*0*	*1.5*
Ave. 1948	*6*	*5.5*			

when spring quadrats are also considered). Quadrat data from August to December are classified as fall data here. For six of the years, results were available from more than one quadrat and the figures are averaged for those years (Table 2). Figure 1 represents these yearly trends in relative populations.

It may be noted that in the fall of 1942 when *Microtus* numbers were at an extreme high, *Blarina* numbers were relatively low. In the following year, 1943, *Microtus* numbers were relatively low, but *Blarina* numbers had doubled. By 1946, when population data were again available, vole numbers had risen to a moderate high and shrew numbers were at the 1943 level. In 1947, *Microtus*

numbers were again at a low point, but *Blarina* numbers had increased to a point almost four times that of 1942. *Microtus* numbers in 1948 showed very little increase over the low of the previous year, but *Blarina* numbers had steadily increased to a point almost equaling the vole population and almost six times the shrew population of 1942. In 1949 *Microtus* numbers continued to be low, but *Blarina* numbers had dropped only slightly from the extreme high of the previous year. The spring of 1950 saw the *Microtus* population at an extreme low point when no voles were taken on a quadrat. At this time *Blarina* populations were

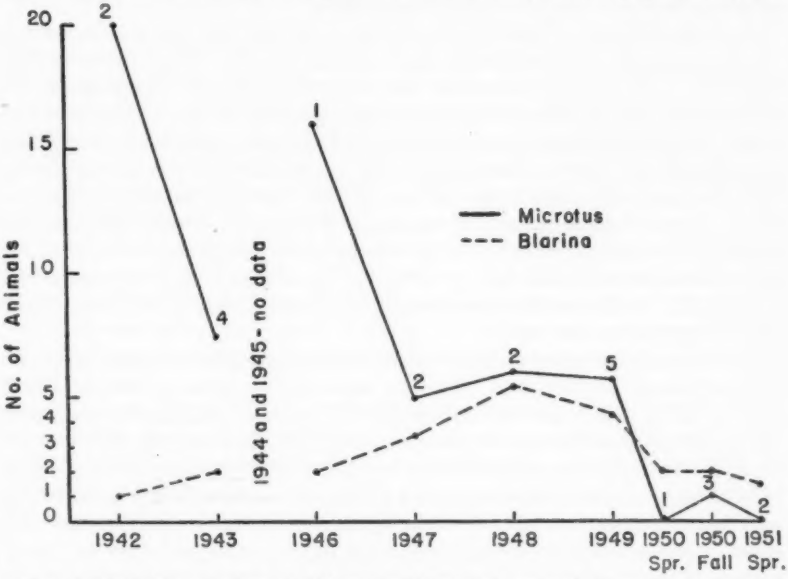

FIG. 1.—Relative numbers of *Microtus* and *Blarina* trapped from one-quarter-acre quadrats in initial 24-hour periods in various years. Fall populations only except for 1950 and 1951. Numbers at points indicate number of quadrats averaged for the period.

at a fairly high level for this time of year. By the fall of 1950 vole numbers had increased only slightly and represented an extreme low for that season of the year in these areas. Shrew numbers at this time showed no increase over spring figures although continuing to exceed vole densities, since twice as many shrews as voles were taken from the quadrats. The spring of 1951 showed vole numbers at a continued extreme low point while shrew numbers persisted at a substantial level for post-winter populations.

Two-day, accumulated catches are available from quadrats of 1947 and 1949 and emphasize further the disproportionate numbers of shrews and voles that were present on these areas. In 1947 the total two-day catch of shrews averaged 7.5 for two quadrats while the total catch of voles averaged only 5.5. In 1949 the two-day total catch for five quadrats averaged 6 shrews and 6 voles. Thus, a

situation existed from 1947 through 1950 where the predator population seemed to exceed or approximate that of the prey. In assessing these relative population figures, however, it should be recalled that short-tailed shrews are apparently wider-ranging mammals than meadow voles (Blair, 1940) and, therefore, shrews from a somewhat larger area may have been exposed to the traps in the quadrats than was the case with *Microtus*. Thus, absolute density ratios might show a higher proportion of voles per unit area. This fact, nevertheless, does not invalidate the relative figures from year to year or hide the strong upsurge in shrew numbers that was a reality during that period.

Field observations.—Observations at nests, runways, and quadrats in the field shed some additional light on this shrew-vole relationship. Descriptions of three nest sites on the study areas, which were surrounded by the remains of meadow voles, have been described in a previous report (Eadie, 1944). In March of 1947 a nest of typical *Microtus* construction was found under a prostrate, rotting fence post. Patches of *Microtus* fur and skin were found scattered in a runway leading from the nest which also contained four *Blarina* scats. These scats, when analyzed, consisted almost entirely of vole hair and bones. On several other occasions typical over-winter *Microtus* nests have been found which seemed to show evidence of shrew usurpation and occupancy. This was indicated by accumulated food remains in the form of opened snail shells, beetle elytra, and by accumulated shrew droppings at the site.

Consideration of two individual quadrats will emphasize the disproportionate ratios of shrews to voles that existed on some of these areas in 1947 and 1948. In October of 1947 a quadrat was established in heavy, matted timothy cover, an apparently ideal habitat for meadow voles. The total two-day catch on this quadrat was 7 *Microtus* and 10 *Blarina*. In October of 1948, a quadrat in the same type of cover yielded 3 *Microtus* and 9 *Blarina* in one day. The possibility that such heavy populations of this extremely active, insatiable predator had some effect on the numbers of voles in these areas from year to year deserves consideration. In this connection, it may be noted from data previously reported (Eadie, 1944) that one, or possibly two, shrews were estimated to have consumed a minimum of 9 voles over one winter period. This was based on actual remains found beside a shrew nest. Shull (1907) found the remains of 23 voles near a *Blarina* nest.

There are indications that high shrew numbers were not sharply localized in some of the years discussed. Shapiro (1950), working near Syracuse, New York, removed 132 *Blarina*, but only 106 *Microtus*, from a 13-acre plot during a period of three months of continuous trapping from June to September 1948. In December and January of 1949 live-trapping for *Microtus* was conducted on several areas within a radius of 10 miles of Ithaca. During that period, while only 7 *Microtus* were taken, the traps yielded 40 *Blarina* specimens or almost six times as many shrews as voles.

Discussion and summary.—It has been shown that meadow voles formed a significant portion of the fall and winter diet of short-tailed shrews on these experimental areas in every year studied for five separate years during the period

from 1942 to 1950. It is not possible to conclude definitely on the basis of these limited data that a direct connection exists between the relative vole and shrew numbers on these areas, but an interesting situation is indicated where a prolonged depression in vole numbers was accompanied by a sustained elevation of shrew numbers at an unusually high level on these study areas, a situation in which shrew numbers seemed to approximate, or, in some cases, to exceed resident vole populations. On the basis of other studies (Hamilton, 1937; Elton, 1942) a cyclic high in mouse numbers could have been expected on these areas three or four years after the 1946 high, but this did not materialize. The possible factors delaying the expected rise in vole numbers may be many and unknown, but the possible significance of sustained high numbers of this diminutive predator on such areas cannot be ignored. It is interesting to note the parallel between this study and some of the findings of a recent study of raptor predation (Craighead and Craighead, 1950). One of the ideas gained was that, at times, "predation as one factor of environmental resistance can be the chief limiting factor in determining prey population levels." *Microtus* was one of the principal prey species involved in that study.

Pearson (1942) demonstrated that the short-tailed shrew is apparently unique among American mammals in the production of a poisonous secretion from the submaxillary salivary glands and that this poison is fully capable of immobilizing mice and voles when transmitted by biting. Such equipment would seem to make this shrew an extremely efficient predator without parallel among mammals as far as known.

It is suggested that such relatively disproportionate population ratios as were found in this study of shrew-vole predation, between an active, highly metabolic, and peculiarly equipped predator and its prey may present a special situation where the numbers of the predator may have an important influence on the numbers of the prey species from year to year.

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A CRANIOMETRIC STUDY OF THE NORWAY RAT

By Joseph Gentile

The taxonomist using external characteristics and cranial measurements often partially bases the descriptions of new forms on variations in mean measurements of different samples. He is generally confronted with a scarcity of data on the amount and kind of variation due to development and sex. The development of a specimen is frequently approximated as juvenile, sub-adult, or adult, by cursory examination using poorly defined or unpublished criteria.

It is the purpose of this paper to describe the variation found in the skulls of the Norway rat, *Rattus norvegicus* (Berkenhout) from a segment of Baltimore, Maryland.

Acknowledgments.—It would be impossible to list in order of importance those people that unselfishly gave their time and advice in order that the completion of this study could be realized. Therefore, the author expresses his sincere gratitude to those listed alphabetically below: Dr. David E. Davis of the Johns Hopkins University made the skulls available and offered suggestions in the preparation of the manuscript; Miss Elaine Diacumakos prepared the illustrations; Mr. Henry C. Eichhorn, Jr., of the Natural History Society of Maryland assisted with the use of the statistics involved; and Miss Joyce C. Lubbert performed most of the routine of readying the data for calculation.

Materials and methods.—The skulls used in this study were obtained during the summer of 1948 from rats captured by the Vertebrate Ecology Division of the Johns Hopkins University School of Hygiene and Public Health. The rats were living in the back yards of row houses in city blocks. Shelter was afforded by burrows in the soil, holes in concrete, debris, or parts of the houses themselves. Most of the yards were bordered by wooden fences which frequently had runways through them. Garbage was the principal source of food.

Because a large number of skulls was obtained and a minimum of time was available for cleaning them, a rapid method of preparation had to be adopted. Although inefficient to the extent that some disarticulation of the zygomatic arches, nasals, and tympanic bullae was encountered, and that the skulls of very small animals were destroyed entirely, the following method was used. At the end of three days of maceration in water, the skulls were boiled in a solution of water, household ammonia, soap, and potassium nitrate until the muscles were soft enough to be removed by a stream of water. A few of the skulls were later cleaned by dermestid beetles.

Measurements to the nearest tenth of a millimeter were taken with a vernier caliper. Error was reduced by using the same instrument throughout and by taking all measurements myself. The same measurement was taken on ten skulls in succession, to introduce further constancy into the technique.

Size group criteria.—From the beginning it was obvious that variations in size as well as those attributed to secondary sexual characteristics should be considered. Arbitrary criteria were set up for the definition of three size groups which are described below and are hereinafter referred to as Group A, Group B, and

Group C. Group A theoretically contained the youngest animals, Group B those of an intermediate age, and Group C the oldest. The assigning of the skulls to the proper groups was done by the author as carefully as possible. The skulls were first divided into the three groups mentioned, then the individuals were critically examined to determine their proper status.

These groups were defined to show three progressive stages in the development of the skull of the Norway rat. No attempt was made to determine the exact ages represented by these groups. Theoretically, it would have been possible to take cage-raised rats and associate the development of their skulls with their chronological age. However, there would be considerable variation in the development and growth rates between wild and caged Norways, since it is known that factors other than simple chronology enter into the development of an organism. Since the extent of the influence of factors such as social position, environment, nutrition, and heredity, in the development of the skull of this species, is not known, it was decided that an attempt to associate cranial development with chronology would be unwise at this time. It is hoped that the importance of such factors will be clarified during the course of future work.

Specimens were assigned to Group A on the basis of the following morphological conditions: upper molars showed rather peaked or pointed tubercles presenting a roughened grinding surface; supraoccipital ridges were present as slightly elevated structures continuing posteriorly as the parietal ridges to the lambdoidal ridge as thin moderately prominent convex crests; the contour of the brain case, from a dorsolateral view, was quite rounded. An imaginary line running along the dorsal surface of the median sagittal plane of the skull appeared as a continuous curved line unbroken by the junction of the parietals and interparietal.

In Group B cranial development was intermediate between Groups A and C, and assignment was based on the following characteristics: tubercles of upper molars noticeable, presenting a mildly roughened grinding surface, wear intermediate between Groups A and C; supraoccipital ridges about twice as thick as in Group A, noticeably elevated, and extended posteriorly as the parietal ridges in a line that still exhibited a great deal of the convexity of Group A; the skulls retained much of the roundness of those in Group A as evidenced by the persistence of the convexity in the parietal ridges. The imaginary line running along the dorsal surface of the median sagittal plane presented the beginning of the formation of the lower plateau formed by the interparietal discussed below under Group C.

Group C contained the most highly developed skulls, and those belonging therein were selected with regard to the following criteria: upper molar tubercles no longer in existence; grinding surface of the molar tooth row almost or (in most cases) entirely flat; supraoccipital ridges present as highly elevated thickened structures and continued posteriorly in a straight line as the parietal ridges which were also highly elevated and thickened; parietal region almost or entirely flattened; when laterally viewed, an imaginary line passing along dorsal surface of median sagittal plane appeared as two slopes at the junction of parietals and interparietal; interparietal appeared as a plateau below the parietals.

Figure 1 illustrates the three stages of cranial development with reference to the size group criteria.

Cranial dimensions.—The graphic method of Dice and Leraas (Contr. Lab. Vert. Gen., Univ. Mich., 3: 1–26, 1936) for comparing a series of means was employed to exhibit the statistically significant differences in the mean measure-

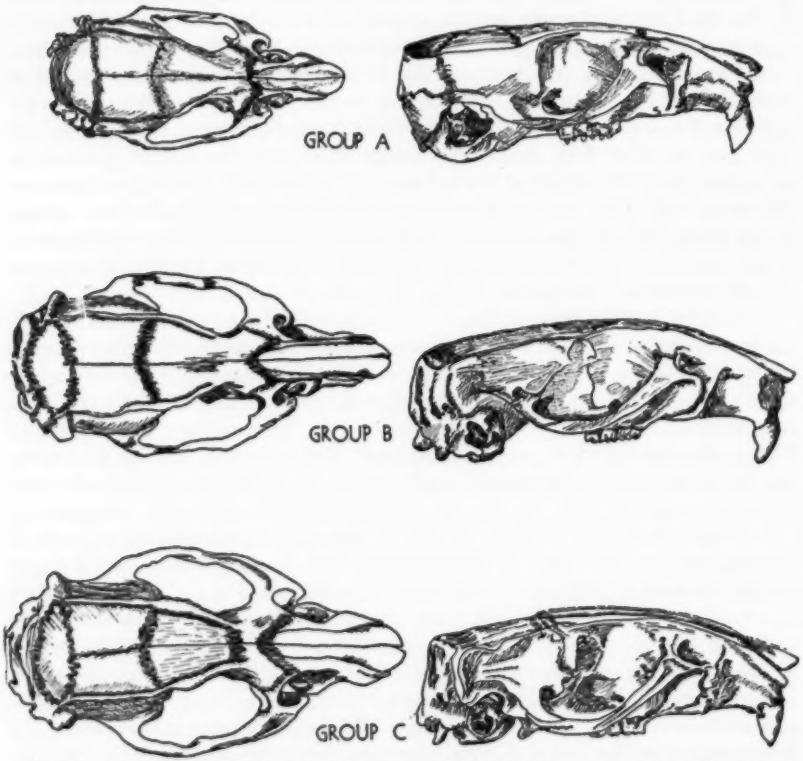

FIG. 1.—Skulls typical of the three size groups. Note, the progressive wear on the molars, the development of the supraoccipital and parietal ridges, and the formation of the interparietal as a plateau below the parietals.

ments of each dimension for each sex and size group. In Figures 2 and 3 the range, means, and twice the standard error of the mean are graphically illustrated. Statistically significant differences are found between comparable samples in which the rectangles indicating twice the standard errors of the means above and below the means do not overlap.

Sexual dimorphism was found only to a limited extent. In Group C, sexual differences in favor of the males existed in palatal length and length of mandible. The length of the mandible in Group B was also significantly larger in the case

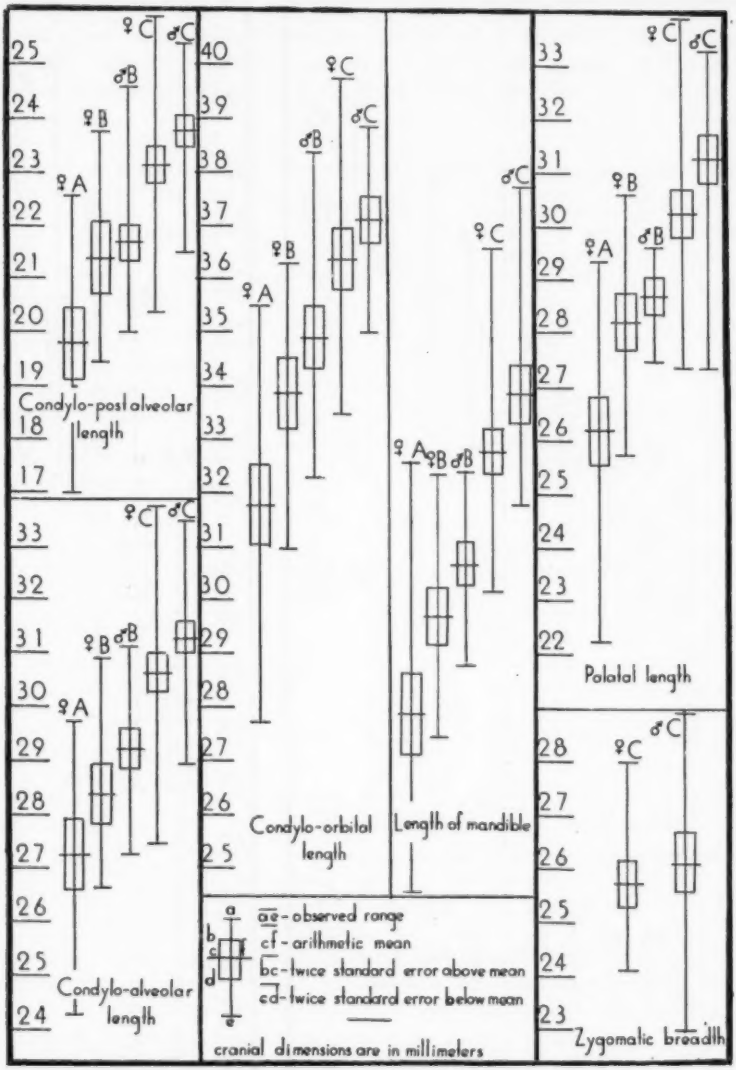

FIG. 2.—Comparison of measurements between size groups and sexes, using method of Dice and Leraas (1936). Statistically significant differences exist between means whose rectangles do not overlap. The males of Group A were not included because of inadequate sample size, and in the case of zygomatic breadth sufficient samples were available only for Group C.

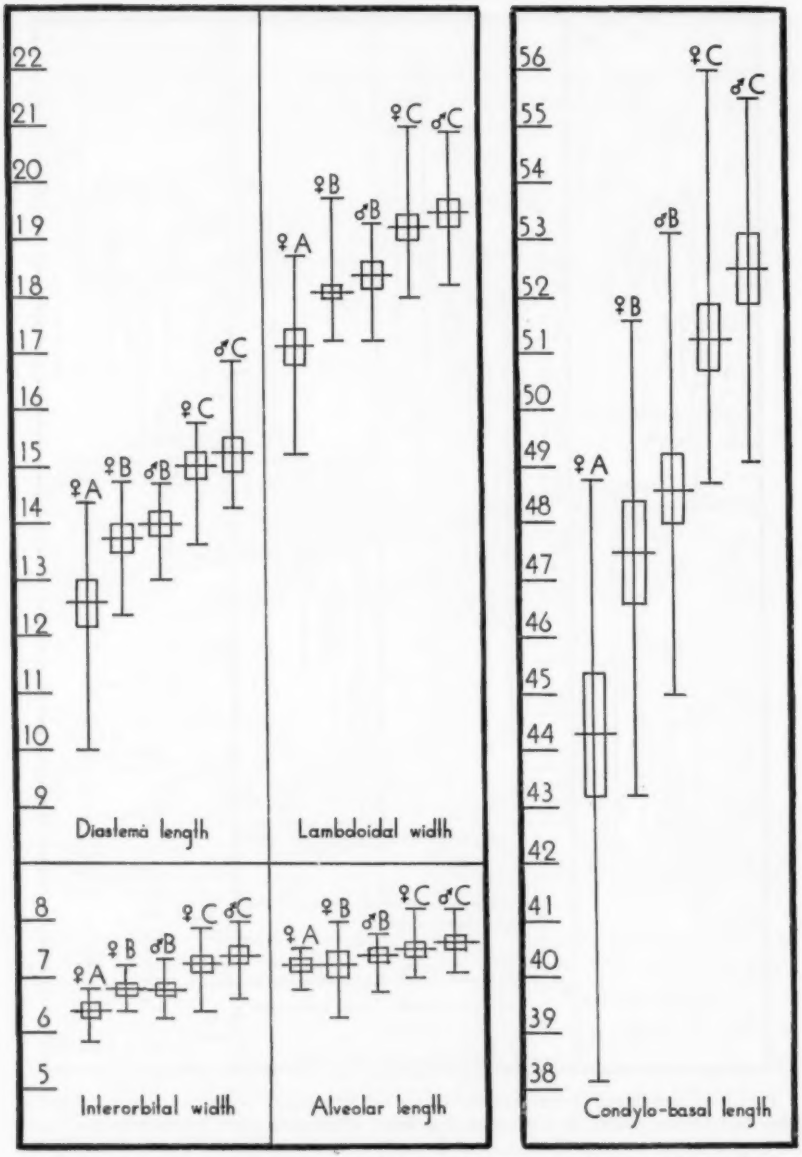

FIG. 3.—Comparison of measurements between size groups and sexes, using method of Dice and Lerass (1936). Statistically significant differences exist between means whose rectangles do not overlap. The males of Group A were not included because of inadequate sample size. Extreme ends of lines indicate range of sample, interior cross bars indicate mean, rectangles indicate twice the standard error above and below the mean.

of the males. There could be no comparison of sexual differences within Group A because of inadequate sample size. It would be well to remember that although these sexual differences in measurements were statistically significant, they could have no value in determining the sex of an unsexed skull, since the differences were so small.

TABLE 1.—*Correlation coefficients between condylo-basal length and other dimensions*

DIMENSION	CORRELATION COEFFICIENTS			
	Frequency	Males	Frequency	Females
condylo-orbital length	86	.91	95	.92
palatal length	79	.99	96	.98
zygomatic breadth	46	.89	51	.45
condylo-alveolar length	78	.97	94	.96
interorbital width	82	.81	96	.89
lamboidal width	78	.89	95	.88
diastema length	75	.85	89	.94
condylo-postalveolar length	76	.57	91	.99
length of mandible	76	.85	92	.92
alveolar length	74	.52	92	.55

TABLE 2.—*Relative growth coefficients of cranial dimensions*

DIMENSION	GROWTH CONSTANTS	
	Males	Females
condylo-orbital length	.54	.85
palatal length	.99	.90
zygomatic breadth	.98	.94
condylo-alveolar length	.80	.83
interorbital width	.37	.59
lamboidal width	.53	.64
diastema length	1.47	1.07
condylo-postalveolar length	1.03	1.01
length of mandible	.86	.97
alveolar length	.22	.34

Significant differences were found to exist between all three size groups in every dimension except alveolar length, where there is a small significant difference between Groups A and C, but with Group B means lying within the limits of the Groups A and C rectangles. In most cases the differences between the sexes in different size groups are appreciably larger than the sexual differences within any one group.

Correlation between dimensions.—Scatter diagrams were employed to determine the applicability of the methods of linear correlation to the data. In all cases the pairs of measurements group themselves as a collection of dots in the pattern of straight lines of varying thickness, with no indication of curvilinear relationship.

In both sexes the scatter diagrams of condylo-orbital length and condylo-basal length appear as two separate parallel ascending lines. There was no apparent explanation for this.

Coefficients of correlation between condylo-basal length and other dimensions have been calculated for each sex and are presented in Table 1. All coefficients are significantly high. P is less than 0.01 in every case. These large coefficients express a high degree of association in the growth of the cranial components, and are probably indicative of the homogeneity of the sample. There seemed to be an expression of sexual dimorphism in the correlation of zygomatic breadth and condylo-basal length. The correlation coefficient for the males is 0.89 and that for the females is 0.45. In the correlation of condylo-postalveolar length and condylo-basal length the males have a correlation coefficient of 0.57 and the females one of 0.99. In the correlation of condylo-basal length and alveolar length the coefficients of correlation, although just as significant as any of the others, are notably smaller. This is probably due to an early cessation of growth in the molar tooth row, which would account for the smaller degree of correlation that exists.

The simple heterogonic growth formula, $Y = bX^k$ was employed to show the rate of change that occurred in the cranial dimensions as the length of skull increased. Values of k (relative growth constants) were computed and are listed for both sexes in Table 2. The methods of Green (Jour. Mamm., 14: 122–31, 1933) were followed in carrying out this phase of the work.

There seemed to be an expression of sexual dimorphism in the relative growth constants. With the exception of length of diastema, whenever large differences in the constants occurred, they were in favor of the females. This was the case in condylo-orbital length, interorbital width, lambdoidal width, length of mandible, and alveolar length. The relative growth constants of length of diastema were 1.47 for the males and 1.07 for the females.

Evidence was found that growth was fastest in the most anterior part of the skulls, as the lengths of diastema, which were the most anterior measurements taken, had the largest relative growth constants. The condylo-alveolar lengths which measured the rest of the skull after the lengths of diastema were taken were quite smaller (males 0.80, females 0.83). The growth constants of the condylo-alveolar lengths were probably inhibited by the slow growth rate of the upper molar tooth row (alveolar length: males 0.22, females 0.34) as the constants of the condylo-postalveolar lengths were also high (males 1.03, females 1.01).

Within each sex, relative growth constants of the measurements of length and width exhibit a relationship with the mean measurements of Group C. In the case of the width measurements, the relative growth constants and means of Group C increase in this order: interorbital width, lambdoidal width, and zygomatic breadth. Among the length measurements, the means increased and the relative growth constants decreased in this order: length of diastema, condylo-postalveolar length, palatal length, condylo-alveolar length and condylo-orbital length. However, this order was reversed in female condylo-alveolar length and condylo-orbital length, as the relative growth constant of the latter was slightly higher than that of the former. The length of mandible was omitted from this

immediate consideration as it was not thought to be a true part of the condylo-basal length, and the alveolar length was also omitted due to an early cessation of development in the molars.

Summary.—A craniometric study of the Norway rat was undertaken to determine the extent of intraspecific variation and sexual dimorphism in three stages of cranial development (three size groups); to describe the qualitative variations that present themselves during the growth process; and to determine the rates of growth in various parts of the skull.

Mean measurements of each dimension for each size group and sex were compared by the use of the graphic method of Dice and Leraas (*loc. cit.*). The heterogonic growth formula was employed to determine the growth rates.

It was found that: (1) Limited sexual dimorphism in the form of larger mean measurements in the case of males of Group C existed in palatal length and length of mandible, and also in length of mandible in Group B. These were the only cases in which the differences were statistically significant, but the dimensions of all males were slightly larger than those of females within each size group. (2) Significant differences existed between means in all three size groups, except in the case of alveolar length. (3) There was a significant degree of correlation between condylo-basal length and the other cranial dimensions (P less than 0.01), along with an expression of sexual dimorphism in the correlation of zygomatic breadth and condylo-postalveolar length. (4) Sexual dimorphism existed in the relative growth constants. Whenever large differences in the constants occurred, the differences were in favor of the females except in length of diastema. (5) Evidence of an anterior growth gradient was found. (6) Evidence was also found of a relationship between the length and breadth mean measurements of Group C and the relative growth constants.

It is concluded that: (1) In taxonomic work with a group of animals it would be prudent to define several stages of development in homogeneous samples before any comparisons are made. (2) In some cases it may be permissible to include male and female measurements in the same series if it is known that no significant degree of sexual dimorphism exists in the measurements taken. (3) Before using differences in relative size of dimensions in respect to condylo-basal length as partial evidence for the description of new forms, it would be wise to determine the changes in relative size characteristic of development.

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AUTUMN FOODS OF CHIPMUNKS AND GOLDEN-MANTLED GROUND SQUIRRELS IN THE NORTHERN SIERRA NEVADA

By Lloyd Tevis, Jr.

The artificial reseeding of burned land in the coniferous forests of western North America is ordinarily nullified by rodents, which remove and devour the seeds. Since the use of poisons, pellets, and physical barriers has not been entirely successful in preventing these depredations (Garman and Orr-Ewing, 1949; Smith and Aldous, 1947), there is need for additional information about the year-round ecology of forest rodents.

Especially important is the effect on animal populations of variations in the seed supply. Conifers are noted for their cycles of fruitfulness and barrenness, and, as Baldwin (1942) asserts, the relation of seed-eating mammals to this periodicity is a fertile field for research, although to segregate the significance of the different factors is not easy.

During the autumn of 1950 most of the conifers of the northern Sierra Nevada of California failed to set seeds, and, coincidentally, the spring-blooming shrubs, having lost their flowers to a late frost, did not produce fruit. The result was a scarcity of seeds on the forest floor.

In some autumns the seeds of woody plants are a major constituent of the rodents' diet. Various investigators, among them Gordon (1943), Holdenried (1940), and Smith and Aldous (1947), have indicated the propensity of the animals for this kind of food, and since it was generally unobtainable during the autumn of 1950, two questions arise. What did the animals eat? What was the effect of the seed shortage on the populations?

Materials and procedure.—This paper reports on the food of four diurnal species of forest rodents: *Eutamias quadrimaculatus* (long-eared chipmunk), *E. townsendi* (Townsend chipmunk), *E. amoenus* (yellow pine chipmunk), and *Citellus lateralis* (golden-mantled ground squirrel). Also it gives a few facts concerning the effect on the animals of that diet.

The study was conducted in the Plumas National Forest of California, and I am indebted to the officers of the United States Forest Service for their co-operation and the many courtesies rendered. The period of field work, from mid-September to the end of October, 1950, covered the terminus of the Californian dry season. At that time chipmunks and squirrels were abundant and active. I observed and collected them at altitudes from 4000 to 6000 feet and in various habitats which included most of the important woody plants of the forest. (Ponderosa pine (*Pinus ponderosa*), Jeffrey pine (*P. jeffreyi*), sugar pine (*P. lambertiana*), White fir (*Abies concolor*), Douglas fir (*Pseudotsuga taxifolia*), incense cedar (*Libocedrus decurrens*), black oak (*Quercus kelloggii*), bitterbrush (*Purshia tridentata*), desert mahogany (*Cercocarpus ledifolius*) mountain whitethorn (*Ceanothus cordulatus*), deer brush (*C. integerrimus*), squaw carpet (*C. prostratus*), silktassel (*Garrya fremontii*), Pinemat manzanita (*Arctostaphylos nevadensis*), greenleaf manzanita (*A. patula*), whiteleaf manzanita (*A. viscida*), and sagebrush (*Artemisia tridentata*))

Information about the food is based on the examination of 314 stomachs, distributed among the species as follows: *E. quadrimaculatus*, 126; *E. townsendi*, 78; *E. amoenus*, 39; and *C. lateralis*, 71. The object of the study was to obtain a broad rather than a detailed picture of food habits, and by examining stomachs in the laboratory simultaneous with work in the field it was possible to attain this goal.

For each habitat studied, a reference collection of seeds and other possible food items was assembled and a list of the important plants compiled. Some of the plants and insects were fed to caged animals so that autopsy would reveal the appearance of the food after it had been ingested. In addition, foraging rodents were watched in the field with binoculars, and the composition of middens was recorded.

Then with dissecting and compound microscopes I examined the contents of fresh stomachs of wild chipmunks and squirrels, making no attempt to identify specifically every item, but determining the main types of food (seed, fruit, root, leaf, fungus, insect, etc.) and noting the presence or absence of coniferous material. Seeds of conifers were recognized easily because their inner coats remained more or less intact. Many other kinds of seeds, including those of manzanita and desert mahogany, were identified in the same way.

Stomach analyses.—Figure 1 gives the percentage volume and the percentage frequency of occurrence of the main types of food in the stomachs of chipmunks and squirrels. Most of the seed material was from herbaceous plants. No coniferous seeds were eaten by *E. amoenus* or *C. lateralis*. One stomach of *E. quadrimaculatus* showed a trace of Douglas fir seed, and ten per cent of the stomachs of *E. townsendi* contained small amounts of seeds of the Jeffrey pine. These figures are in striking contrast with those of Smith and Aldous (1947), who counted 796 jack pine seeds in the stomach of a chipmunk, and of Gordon (1943), who recorded 332 lodgepole pine seeds in a pair of cheek pouches.

Woody plant seeds being scarce in the Sierra Nevada during 1950, Figure 1 indicates that chipmunks and squirrels turned to fungi for their chief source of food. Although sporophores of the Agaricales were not present until the beginning of the winter rains, the meaty spore-fruits of the hypogeous or subterranean forms of the Gasteromycetes and Tuberales were abundant throughout the dry season. They were sought eagerly by the rodents, which located them in the ground through the strong odors emitted, and then dug them up to eat. I watched this behavior on many occasions. It was similar to the rooting for truffles by trained dogs and pigs in France and England, and in places the floor of the forest was pitted by the diggings.

These hypogeous spore-fruits grow at depths of one to six inches. As a rule they are roughly globular in shape with diameters of an inch or two. Many have dull exteriors, but a few are encased in brightly colored peridia. I suspect that they are a normal component of the diet even when coniferous seeds are plentiful, for Broadbooks (1949) records "basidiomyceteous tubers" as being a food of chipmunks in eastern Washington. Many species of hypogeous fungi inhabit the Pacific Coast of North America, and papers useful for their identification are those by Gilkey (1939) and Zeller (1949).

When warm heavy rains ended the dry season, there was an upwelling over the forest floor of sporophores of the Agaricales. Then, presumably because of the ease with which this surface nourishment could be obtained, the consumption of fungi by rodents increased to even greater amounts. For example, in one locality where I trapped *E. quadrimaculatus* immediately before and after the rains, the frequency of occurrence of fungi in the stomachs rose from 62 to 91 per cent. Most of the kinds eaten belonged to the genera *Clitocybe* and *Boletus*.

Although I recognized fungi in the stomachs by consistency, texture, and odor of the flesh, certain identifications were based on the spores. I do not know

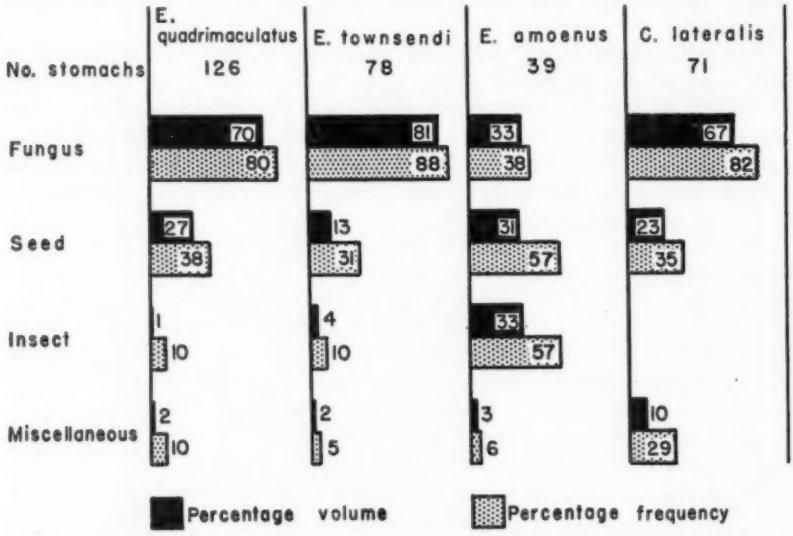

FIG. 1.—Main types of food in stomachs of animals collected between September 15 and October 31, 1950. The width of each vertical column equals one hundred per cent.

whether the spores are viable when discharged from the alimentary canal, but in all probability those of hypogeous forms, being unable to utilize air currents, must depend in part on mycophagous animals for dissemination. In this connection, since mycorrhiza-forming fungi are essential for the growth of many kinds of tree seedlings (Kelley, 1950; Rayner, 1947), an interesting study could be made of the reinoculation of devastated ground by rodents. Wilde, Youngberg, and Hovind (1950) believe that the partial absence of mycorrhizal fungi after beaver-flooded areas have been drained may be the major factor which retards the growth of new trees.

Cheek pouch contents.—Because of the shortage of the seeds of woody plants only a small proportion of the trapped animals carried food in their cheek pouches. The figure for *E. amoenus* was 28 per cent in 46 examples; for *E. quadrimaculatus*, 24 per cent in 125; for *C. lateralis*, 19 per cent in 76; and for *E. townsendi*, 15

per cent in 85. Fungi occurred rarely. Being perishable, like the insect food of chipmunks in Minnesota (Aldous, 1941), they were consumed on the spot.

It is significant that *E. townsendi*, the one species that ate an appreciable amount of coniferous seeds, was the only species to collect them. In 85 pouches of *E. townsendi*, six per cent contained seeds of the Jeffrey pine; the average number of seeds per seed-carrying animal was four, and the maximum eight.

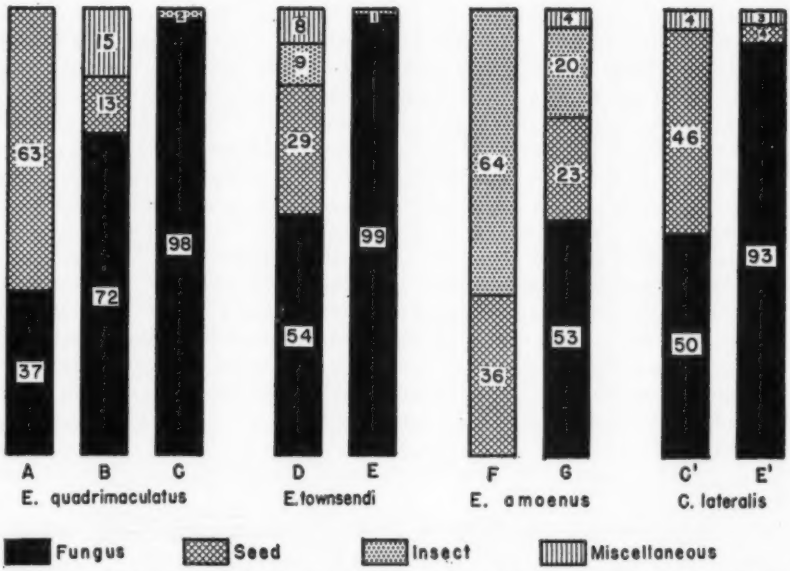

FIG. 2.—Main types of food in stomachs (percentage volume) of animals from different habitats: A, burned conifer forest replaced by black oak and deer brush (20 stomachs); B, burned conifer forest replaced by mixed brush (10 stomachs); C and C¹, logged conifer forest (9 and 18 stomachs, respectively); D, Jeffrey pine-chaparral association (29 stomachs). E and E¹, virgin conifer forest (17 and 16 stomachs, respectively); F, Jeffrey pine-desert mahogany association (14 stomachs); G, ponderosa pine-grassland (17 stomachs).

These facts suggest that this chipmunk is more detrimental to forest regeneration than are the other kinds. *C. lateralis*, for example, did not collect or eat pine seeds even at the same places where *E. townsendi* found them. However, because the latter occurred more often in virgin forests than did the other species, it had the greater opportunity to take coniferous seeds. *C. lateralis*, which was trapped commonly among weeds in heavily logged areas, collected the seeds of *Galium* and bull thistles; *E. amoenus*, which favored the pine-grassland areas, carried the small seeds of forbs, grasses, and sagebrush; and *E. quadrimaculatus*, a brush-lover, collected the nutlets of manzanita and the seeds of deer brush and mountain whitethorn.

Analysis of food by habitat.—Since the variation in content of the cheek pouches

depended on locality, a composite food-picture based on records from a number of places (Fig. 1) is perhaps less significant than analysis of the food by habitats. Although *E. amoenus* appeared to be the chief insect eater, this conclusion is complicated by the factor of availability, for the type of food eaten differed more markedly within a species, according to habitat, than between different species occupying the same area (Fig. 2).

One habitat in which I found *E. quadrimaculatus*—burned conifer forest replaced by black oak and deer brush—offered little food. The acorn crop had failed, only a few seeds of deer brush had been shed, and, because of the lack of duff and humus, fungi were scarce. Under the circumstances, the chipmunks were forced to eat the shells and the desiccated and shriveled meats of acorns left over from the heavy crop of the preceding year (Fig. 2, A). Eighty-two per cent by volume of seed material in the stomachs was of old acorns, the logs and stumps were littered with broken shells left by the rodents, one animal was seen to dig up an old shell and reject it after futile gnawing, and another was trapped while it had a piece of rotten acorn meat in its cheek pouch.

By contrast, in a virgin forest, where the dark soil under the old conifers was rich with humus, the chipmunks (*E. townsendi*) fed extensively on fungi (Fig. 2, E). Although pine nuts occurred in cheek pouches of a few of the animals occupying that forest, none were in the stomachs. Presumably the rodents collected these seeds to store them for future use. But in an open and somewhat arid pine-chaparral association where mushrooms were less abundant, nearly half of the seeds eaten by the same species of chipmunk were of pine (Fig. 2, D). Apparently because of the relative shortage of fungi in this latter habitat, the animals were compelled to consume rather than cache whatever coniferous seeds they could locate.

In virgin forests, *C. lateralis*, like *E. townsendi*, subsisted largely on hypogeous fungi (Fig. 2, E), but in logged areas where weeds had prospered, a higher proportion of the food was of herbaceous seed (Fig. 2, C). At one site, the Old World, autumn-flowering *Cirsium lanceolatum* accounted for 74 per cent of seed material in the stomachs. Often I watched the squirrels climb between the sharp spines of these bull thistles to cut off flower heads and carry them by mouth to a stump, where they extracted the seeds, discarding the bracts and down.

A totally different kind of food was available in a Jeffrey pine-desert mahogany association seriously overgrazed by deer and livestock. An ethmiid caterpillar (H. H. Keifer reported that the caterpillar "belongs in the genus *Ethmia* and probably in the species *discostrigella* (Chambers)"), which defoliates the desert mahogany, existed in enormous numbers and constituted the chief food of *E. amoenus* (Fig. 2, F). To estimate how many pounds of foliage were saved by the insect-eating rodents is not practicable, but as the only important browse for deer and livestock in the area was desert mahogany, it is obvious that a rodent control program at that time would have harmed the range and could not have been justified even as a means of saving coniferous seeds. A month after my original observations nearly all the caterpillars had vanished. Even pupae were rare.

Approximately half the volume of seed eaten by chipmunks in this area was of

desert mahogany, but only the stomachs containing *Ethmia* were distended to maximum size. In passing it may be mentioned that the caterpillar has a unique although apparently not too successful defense against insectivorous rodents. When the branch supporting a larva is tapped lightly, as by the careless steps of a small mammal, the caterpillar instantly rolls off and hangs out of reach at the end of a thread of its own secretion. Later, when the disturbance subsides, the larva returns to the branch via the thread.

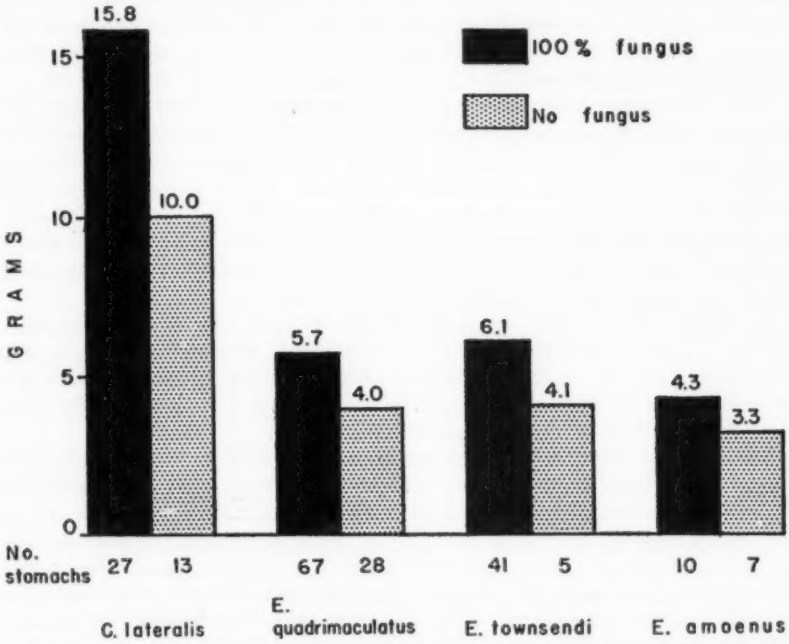

FIG. 3.—Average weights in grams of stomachs containing no fungi and of those containing only fungi (the stomachs of *Citellus lateralis* have greater capacities than those of chipmunks).

Weight of food in the stomachs.—To determine the effect, if any, of the shortage in woody plant seeds on the rodent populations, I studied body weights, the amount of hibernation fat, and the weights of food in the stomachs. Interpretation of the weights of food in stomachs of wild rodents is complicated by many factors. Nonetheless, such weights are a rough measure of the availability of food. For example, if an animal can obtain unlimited quantities, it will gorge to repletion and the stomach will be heavy and distended. But if food is not abundant or if of a kind that is disliked or that must be laboriously extracted (such as endosperm within the hard nutlets of manzanita), the stomach will be relatively light.

Figure 3 illustrates this fact by comparing the average weights of stomachs with

and without fungus. Clearly, the mycophagous individuals ingested greater amounts of nutriment. (The stomach of one squirrel filled with the remains of hypogeous sporophores accounted for a fifth of the animal's weight!) As a corollary, it can be stated that the rodents which fed most bountifully lived where there was a wealth of subterranean fungi.

If fungi were scarce the amount of food taken was relatively small. For example, in the burned conifer forest where *E. quadrimaculatus* ate year-old acorns for lack of other subsistence (Fig. 2, A), the average weight of food in the stomachs was conspicuously less than the average from any other habitat and almost half the average from logged areas. I conclude, therefore, that the area did not produce sufficient nourishment for the chipmunks during the fall of 1950.

Body weights and hibernation fat.—Since the average amount of food in the stomachs varied with habitat, it seemed likely that the bodies of individuals from fertile regions would be the heaviest. To test this hypothesis, comparable body weights were obtained by subtracting the stomach weights. I learned then that until mid-October the average body weights, corrected and analyzed for each species by sex and age classes, did not differ between habitats. Individuals which had lived amid a profusion of underground fungi were not heavier than those which had lived where there was little food.

A pronounced contrast in weights from different areas appeared during mid-October, however, when the chipmunks (excluding *E. amoenus*) began to aquire hibernation fat. The reason was that in areas where fungi were abundant the animals became fat sooner than they did elsewhere. One example of this phenomenon is rather striking although based on small numbers of specimens.

Two adjacent areas originally covered by mixed conifer forest differed in that one had been burned and the other logged. In the latter area, the chipmunks (*E. quadrimaculatus*) fed almost entirely on hypogeous fungi (Fig. 2, C), but in the burned area where fungi were relatively scarce, animals of the same species ate a greater amount of the leaves and seeds of herbaceous plants (Fig. 2, B). The mycophagous population of the logged area was the more prosperous, the average quantity of food eaten being twice that of the burned area and the corrected body weights about twenty per cent higher for each of the sex and age classes.

In addition, all nine individuals from the logged area had some hibernation fat, two having heavy deposits, while six of ten animals from the burned area had no fat and not a single individual showed a heavy deposit. In short, where hypogeous fungi were abundant the chipmunks acquired hibernation fat; but where food was scarce the acquisition of fat was retarded, and the chances that the animals on those areas would survive the winter were diminished.

My conclusion, then, is that during the fall of 1950 the successful populations lived where hypogeous fungi flourished. Those fungi, besides being palatable, are a nutritious food, high in protein content, and since they occurred abundantly on most areas occupied by the chipmunks and squirrels, they neutralized any deleterious effect of failure of the seed crops. This conclusion, however, does not consider the effect of seed failure on rodent reproduction. The fact that the sexual organs of the chipmunks enlarged and became increasingly vascular when the

animals entered hibernation indicates that the autumn food may influence the spring reproduction. Furthermore, the importance of storable items of food, such as coniferous seeds, may not be apparent until the animals emerge from hibernation in the spring and begin searching for their autumn caches.

Summary.—The 1950 seed crop of conifers and shrubs in the northern Sierra Nevada was a failure.

In lieu of the seeds of woody plants, the four species of diurnal rodents studied (*Eutamias quadrimaculatus*, *E. townsendi*, *E. amoenus*, and *Citellus lateralis*) turned to the sporophores of hypogeous fungi for food.

The relative amount of fungi consumed varied with the habitat. In some areas where fungi were scarce, the animals ate material which otherwise would have been ignored. In other places, fungi constituted practically all of the diet.

Individuals unable to obtain fungi ingested a smaller amount of food as shown by the fact that stomachs without fungi weighed less on the average than those containing only fungi.

Average body weights did not differ between habitats until the time of hibernation. Then those individuals living where hypogeous fungi flourished became fat and heavy.

Since hypogeous fungi were obtainable in large amounts on most ground occupied by the rodents, the population as a whole did not appear to suffer from failure of the seed crop. The effect, though, on reproduction will not be apparent until the spring months.

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FOOD CONSUMPTION IN *PEROMYSCUS* IN RELATION TO AIR TEMPERATURE AND PREVIOUS THERMAL EXPERIENCE

By John A. Sealander, Jr.

There is general agreement in the literature that the rate of food consumption in mammals varies inversely with the environmental temperature (Chenoweth, 1917; Schwabe, Emery, and Griffith, 1938; Mills, 1944; Dugal and Therien, 1947), but little or no mention is made of the length of time required for mammals to adjust their rate of food intake to altered environmental temperatures. In any comparison of different measurements of food consumption rate for the same species, then, not only the temperature of measurement but also the previous thermal history of the animal must be considered.

The rate of food consumption and kind of food eaten may also be affected by other factors than temperature per se. Chew (1951) demonstrated that for *Peromyscus leucopus noveboracensis* a normal rate of food consumption was dependent upon a normal supply of drinking water. This would not hold of course for mice which normally get their water from food or metabolically. In nature mammals may instinctively select those foods which best enable them to withstand the particular conditions of temperature to which they are normally exposed. This matter of choice in relation to environmental temperature has been investigated by Leblond, Dugal, and Therien (1944) and Dugal, Leblond, and Therien (1945) who found that in the cold rats will choose a diet composed of about 25 per cent protein, 25 per cent fats, and 30 per cent carbohydrates. At high temperatures consumption of glucose increased, reaching a level of nearly 70 per cent, while consumption of lipids decreased. Salt consumption increased in the cold.

With an increase in rate of food consumption at low temperature there may also be a decrease in digestive efficiency (Brody, 1945: 76–85, 246; Quimby, 1948) and less selectivity in feeding than at high temperatures (Hatfield, 1940).

Methods.—Specimens of *Peromyscus leucopus noveboracensis* (Fischer) were taken from wild populations in the vicinity of Champaign-Urbana, Illinois, while specimens of *Peromyscus maniculatus austerus* (Baird) were furnished by Dr. B. T. Ostenson, Pacific Lutheran College, Parkland, Washington, who trapped them from wild populations. Individuals of *Peromyscus maniculatus bairdi* (Hoy and Kennicott) were reared from birth in the laboratory and were used for experiments after they had reached the age of 5–6 months. All animals used in this study were kept in a thermostatically controlled room at temperatures from 20–24°C. for a period of about one month before using experimentally.

In the determination of food consumption for *noveboracensis* the mice were kept in small circular cages of the type described by Chew (1951). Food in pellet form was provided in a side chamber behind a one-half-inch-mesh partition which permitted the mouse to eat through the mesh, but did not allow food to be removed to the cage proper where pieces would be lost. Food residue fell into a detachable tin pan beneath the side chamber from which it was recovered and weighed.

A large quantity of food was exposed to the temperature and humidity condi-

tions of measurement for several days before the start of each experiment to allow the water content of the food to equilibrate with room conditions. Weighed amounts of this food were given each mouse, the residue from feeding collected, and the air-dry weight of food consumed was determined at 48-hour intervals. Samples of food were removed at intervals of four to five days, weighed and placed for 48 hours in a drying oven at 100–102°C., and then reweighed to determine the water content. The percentage, 100 times air-dry weight minus absolute-dry weight divided by air-dry weight, then represented the water content of the food. The air-dry weight of food consumed by each mouse then was corrected to absolute-dry weight every four or five days.

Food was weighed to an accuracy of .01 gram on a chainomatic balance. Animals were weighed at the same time every fourth day on a balance accurate to 0.1 gram.

Drinking water was provided to all animals (*ad libitum*). All animals were fed (*ad libitum*) on Purina Laboratory Chow which had a caloric value of 4.26 Calories per gram dry weight.

Food consumption was measured somewhat differently for *bairdi* and *austerus*. These subspecies were confined individually in ordinary wire-mesh laboratory cages. Food pellets were placed inside a round, half-inch wire container, with a diameter of about two inches and a height of about three and one-half inches, soldered to the bottom of a galvanized metal pan three-fourths inch deep and four inches square. Food was eaten through the mesh and the residue from feeding collected in the square metal pan. Feces dropped into the pan were easily separated from the residue and did not accumulate to any extent due to the habit of *bairdi* and *austerus* of defecating in one corner of the cage. The hopper filled with food was weighed at the beginning of each experiment and at five-day intervals thereafter, being refilled when necessary and when the mice were shifted from one environmental temperature to another. The weight difference between successive weighings represented the weight of air-dry food consumed for each five-day period, corrected as before for moisture content of the food.

To test the relative accuracy of the two methods of measurement, two *bairdi* were first kept at 19.5° to 21.5°C. for a 12-day period, at the end of which their rate of food consumption was presumably adjusted to the environmental temperature. Food consumption of each mouse then was measured by each method on alternate days over a period of 12 days at the same range of air temperature. No significant difference in food consumption by either method could be determined.

In order to determine the effect of temperature on food consumption, as well as the effect of previous thermal experience, the following procedure was adopted. Two groups of mice of each subspecies were first placed at a low (6.0°–10.5°C.) and a high (29.5°–32.5°C.) temperature, and food consumption was measured over a period of 30 days. All of these mice had been previously subjected to room temperatures ranging from about 20–24°C. for four to five weeks. After measuring food consumption at low and high temperatures both groups of mice were removed to the same intermediate temperature (19.5°–21.5°C.) range, and food

consumption was again measured over a 30-day period. Following this period of measurement, the groups which had first been placed at a low and high temperature were reversed and placed at high (29.5°–32.5°C.) and low (6.0°–10.5°C.) temperatures, respectively. Food consumption was measured as before over a 30-day period. The food consumption of each mouse in a group, except for *austerus* where food consumption of the entire group was measured, was measured individually. Food consumption of each group was then computed from the individual food consumptions.

Relative humidities in each range of temperature were measured at four-day intervals with a cog psychrometer.

Results and discussion.—Food consumption for *noveboracensis*, *bairdi*, and *austerus* varied inversely with air temperature. Lowering of environmental temperature was accompanied by increased food consumption (Tables 1, 2, 3, 4, and 5; Fig. 1). More food was eaten per day by *noveboracensis* at all air temperatures than by *bairdi* or *austerus*. However, caloric intake per gram body weight per day was greater for *bairdi* at all temperatures than for *noveboracensis*, while caloric intake per gram body weight per day for *austerus* was lower than that of *noveboracensis* and *bairdi*. Pregnant *noveboracensis* ate more at both high and low temperatures than did non-pregnant females.

The smaller caloric intake per gram body weight of *noveboracensis* would be expected in view of its larger size, as compared with *bairdi*, with a smaller proportional surface area for heat loss. The low caloric intake per gram body weight of *austerus* with its low rate of total food consumption may have been due to increased digestive efficiency.

Dice (1922) also found that *noveboracensis* ate more food than *bairdi* at equivalent temperatures, and that caloric intake per gram body weight was only slightly larger for *bairdi*. He attributed a lower food consumption at high temperatures to a smaller heat loss at those temperatures. It was also noted that pregnancy and lactation increased food consumption. Hatfield (1940) found no noticeable correlation between temperature and food consumption in *bairdi*, while Chenoweth (1917) noted that food consumption of *noveboracensis* varied inversely with the temperature.

An initial adjustment in rate of food consumption occurred for all three subspecies when subjected to a sudden lowering or raising of environmental temperature. Lowering the air temperature increased the rate of food consumption for a time, but it then levelled off or declined slightly. This period of adjustment varied with individual mice, but in most cases was completed in from 8–12 days and averaged about 10 days for each group. Elevation of air temperature produced a downward adjustment in rate of food consumption of *bairdi* and *austerus* which levelled off and then in some cases underwent a slight increase. The period of adjustment varied with individual mice, but was not so rapid as adjustment to lowered temperatures, ranging from about 10–20 days with an average of around 15 days for each group. In *noveboracensis* an upward adjustment in rate of food consumption occurred during the first 10 days at high temperature (Fig. 1). This was in contrast to the gradually decreased appetites of *bairdi* and *aus-*

TABLE 1.—*Food consumption of P. l. noveboracensis in relation to air temperature, previous thermal experience, and duration of exposure to a given range of temperature*

ANIMAL NUMBER AND SEX	AVERAGE AIR TEMPERATURE (°C.)	AVERAGE RELATIVE HUMIDITY (PER CENT)	AVERAGE GRAMS DRY WEIGHT OF FOOD CONSUMED PER DAY (DAYS)				AVERAGE CALORIC INTAKE PER GRAM PER DAY (DAYS)			
			0–10	10–20	20–30	0–30	0–10	10–20	20–30	0–30
	8.5	66.7	3.33	5.32	5.34	4.66	.489	.809	.846	.709
1♂	20.5	43.6	3.48	3.63	3.79	3.63	.539	.539	.547	.541
	30.5	28.3	2.98	2.98	2.59	2.85	.444	.456	.386	.444
	8.5	66.7	5.87	6.26	5.99	6.04	1.127	1.165	1.144	1.144
2♀	20.5	43.6	4.90	3.84	4.16	4.30	.971	.787	.844	.868
	30.5	28.3	2.63	2.30	2.50	2.48	.541	.480	.533	.518
	8.5	66.7	6.11	7.60	6.92	6.88	.936	.984	1.003	.980
3♀*	20.5	43.6	5.61	5.04	4.19	4.95	.888	.839	.708	.814
	30.5	28.3	3.20	3.08	2.69	2.99	.568	.578	.498	.547
	8.5	66.7	7.46	8.29	6.98	7.58	1.096	1.275	1.152	1.170
4♀†	20.5	43.6	6.71	5.24	3.99	5.31	1.181	.950	.714	.950
	30.5	28.3	2.86	2.40	2.38	2.54	.523	.458	.455	.477
	8.5	66.7	6.03	6.61	6.18	6.28	.895	1.002	1.041	.973
5♀	20.5	43.6	4.84	4.52	4.25	4.54	.799	.735	.739	.758
	30.5	28.3	3.26	2.79	2.89	2.98	.567	.526	.485	.524
	8.5	66.7	6.69	5.99	5.63	6.10	1.003	.956	.933	.973
6♂	20.5	43.6	3.99	4.27	2.79	3.68	.714	.705	.517	.648
	30.5	28.3	3.19	2.95	2.60	2.91	.550	.454	.383	.459
	30.5	29.3	2.76	3.49	3.31	3.18	.360	.432	.422	.404
7♂	20.5	43.6	3.62	3.42	3.62	3.55	.494	.496	.545	.511
	8.5	65.1	6.93	7.02	6.62	6.86	1.025	1.010	.934	.991
	30.5	29.3	1.98	2.20	2.36	2.18	.367	.432	.493	.426
8♂	20.5	43.6	3.67	4.46	4.48	4.20	.692	.864	.826	.792
	8.5	65.1	5.97	6.98	7.23	6.73	1.096	1.310	1.257	1.225
	30.5	29.3	4.66	3.27	2.60	3.51	.536	.401	.344	.438
9♀‡	20.5	43.6	5.67	5.43	5.16	5.42	.745	.746	.728	.740
	8.5	65.1	6.58	7.28	7.29	7.05	.934	1.020	.996	.985
	30.5	29.3	2.07	2.85	3.36	2.76	.265	.369	.425	.353
10♀	20.5	43.6	3.36	4.07	3.72	3.72	.466	.582	.572	.539
	8.5	65.1	6.26	6.89	6.59	6.58	1.022	1.138	1.127	1.095
	30.5	29.3	2.87	3.25	2.69	2.94	.422	.500	.428	.449
11♀	20.5	43.6	3.93	4.39	4.89	4.40	.637	.739	.857	.741
	8.5	65.1	7.23	7.38	7.22	7.28	1.232	1.200	1.202	1.211
	30.5	29.3	2.53	3.43	3.28	3.08	.479	.619	.613	.573
12♂	20.5	43.6	3.51	3.80	4.18	3.83	.636	.726	.788	.716
	8.5	65.1	6.18	7.08	6.61	6.62	1.213	1.409	1.246	1.288

* Pregnant first 20 days at 8.5°C.
† Pregnant first 12 days at 8.5°C.
‡ Pregnant first 14 days at 30.5°C.

terus, and, although the cause is not clear, may indicate a less rapid initial adjustment to high temperature. Food consumption in the final 20 days of exposure at high temperature still remained well below that during the final 20 days at the intermediate temperature which followed.

TABLE 2.—*Food consumption of P. m. bairdi in relation to air temperature, previous thermal experience, and duration of exposure to a given range of temperature*

ANIMAL NUMBER AND SEX	AVERAGE AIR TEMPERATURE (°C.)	AVERAGE RELATIVE HUMIDITY PER CENT	AVERAGE GRAMS DRY WEIGHT OF FOOD CONSUMED PER DAY (DAYS)				AVERAGE CALORIC INTAKE PER GRAM PER DAY (DAYS)			
			0-10	10-20	20-30	0-30	0-10	10-20	20-30	0-30
	8.5	65.8	5.58	5.59	6.08	5.71	1.151	1.132	1.159	1.158
1♂	20.5	44.0	3.80	3.52	3.69	3.67	.777	.744	.799	.774
	30.5	30.5	3.15	2.64	2.65	2.81	.728	.635	.644	.669
	8.5	65.8	4.59	4.74	4.58	4.63	1.326	1.391	1.293	1.341
2♀	20.5	44.0	3.73	2.67	2.92	3.10	1.049	.732	.773	.847
	30.5	30.5	2.48	1.37	1.81	1.89	.683	.400	.527	.537
	8.5	65.8	6.21	5.34	6.24	5.93	1.459	1.260	1.486	1.419
3♂	20.5	44.0	4.55	4.03	3.71	4.10	1.097	.922	.856	.965
	30.5	30.5	2.95	1.97	1.77	2.23	.728	.496	.458	.562
	8.5	65.8	5.58	5.22	5.37	5.39	1.334	1.243	1.264	1.283
4♀	20.5	44.0	4.20	3.32	3.46	3.66	.944	.740	.767	.816
	30.5	30.5	3.12	2.81	3.06	2.99	.774	.725	.785	.754
	30.5	30.1	2.05	1.60	1.66	1.77	.532	.415	.429	.460
5♀	20.5	44.0	2.70	3.03	3.19	2.97	.670	.747	.786	.735
	8.5	66.4	4.80	5.21	5.07	5.03	1.127	1.184	1.157	1.165
	30.5	30.1	2.89	2.16	2.21	2.42	.702	.511	.510	.570
6♂	20.5	44.0	3.40	3.79	3.86	3.68	.744	.825	.842	.804
	8.5	66.4	6.25	5.92	6.95	6.37	1.298	1.204	1.362	1.292
	30.5	30.1	2.16	2.29	2.37	2.27	.481	.524	.568	.523
7♀	20.5	44.0	3.28	3.37	3.32	3.32	.745	.751	.750	.752
	8.5	66.4	6.02	6.64	6.37	6.34	1.330	1.422	1.329	1.364
	30.5	30.1	2.71	2.59	2.70	2.66	.646	.592	.576	.599
8♂	20.5	44.0	3.43	4.14	4.11	3.89	.747	.904	.927	.859
	8.5	66.4	6.22	7.17	6.89	6.76	1.322	1.472	1.470	1.440

A running average was used to smooth the food consumption curve of *noveboracensis*. Food consumption was measured every 48 hours. The average daily food consumption for each successive 48-hour period was taken as the food consumption for the 1st, 3rd, 5th, etc. days. The food consumption for the 1st, 3rd, 5th, 7th, and 9th days was averaged to give food consumption for the 5th day; the first three values were then dropped and food consumption for the 7th to 13th day was averaged to give food consumption for the 10th day, and so on. Averages

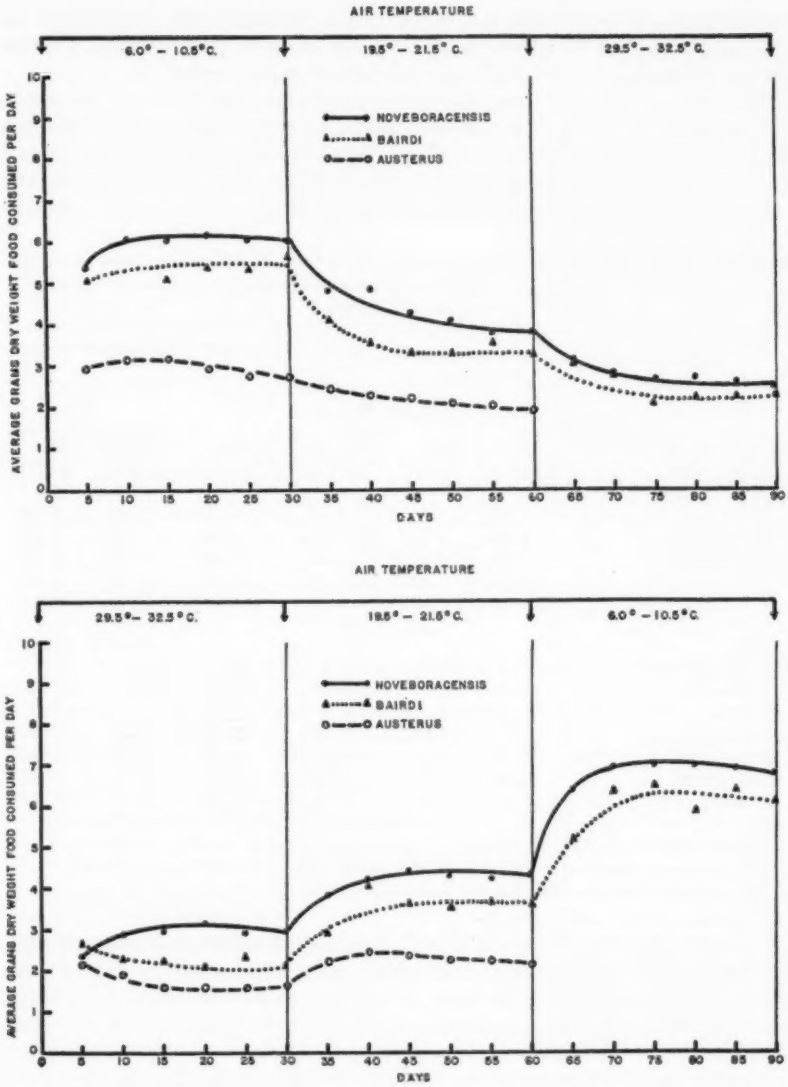

FIG. 1.—Comparison of group averages of food consumption of *Peromyscus* in relation to periodically raised air temperature, *upper*, and periodically lowered air temperature, *lower*.

for the 29th, 59th, and 89th days were used to represent food consumption on the 30th, 60th, and 90th days, respectively, in order to avoid averaging values for food consumption at different environmental temperatures.

The effect of previous thermal experience upon the rate of food consumption of *noveboracensis*, *bairdi*, and *austerus* is shown by comparison of group averages of food consumption in the intermediate range of temperature (Tables 3, 4, and 5, Fig. 1). Animals previously exposed to high temperature for 30 days increased their food consumption; the reverse was true for animals exposed to low tempera-

TABLE 3.—*Comparison of food consumption of two groups of P. l. noveboracensis in relation to air temperature, previous thermal experience, and duration of exposure to a given range of temperature*

	AVERAGE DRY WEIGHT OF FOOD CONSUMED PER DAY (GRAMS)			AVERAGE CALORIC INTAKE PER GRAM PER DAY		
	Group I†					
Average temperature, °C.*	8.5 (66.7)	20.5 (43.6)	30.5 (28.3)	8.5 (66.7)	20.5 (43.6)	30.5 (28.3)
0–10 Days	5.92	4.92	3.02	0.929	0.849	0.532
10–20 Days	6.68	4.42	2.75	1.032	0.759	0.492
20–30 Days	6.37	3.86	2.61	1.020	0.678	0.457
0–30 Days	6.26	4.40	2.79	0.990	0.736	0.492
	Group II‡					
Average temperature, °C.*	30.5 (29.3)	20.5 (43.6)	8.5 (65.1)	30.5 (29.3)	20.5 (43.6)	8.5 (65.1)
0–10 Days	2.81	3.96	6.53	0.405	0.612	1.087
10–20 Days	3.08	4.26	7.11	0.459	0.692	1.181
20–30 Days	2.93	4.34	6.93	0.454	0.719	1.127
0–30 Days	2.94	4.19	6.85	0.441	0.673	1.133

* Mean relative humidity, per cent, in parentheses.
† Six animals, measurement started in 6.0–10.5°C. range.
‡ Six animals, measurement started in 29.5–32.5°C. range.

tures for an equal length of time. The rate of food consumption of animals with a warm thermal history reached a higher plateau after about 15 days at the intermediate temperature than that for animals with a cool thermal history. This was true for all subspecies compared. Furthermore, when animals that were initially subjected to high temperatures were placed at low temperatures, after 30 days at the intermediate temperature, the rate of food consumption for both *noveboracensis* and *bairdi* reached a noticeably higher level than for animals not previously exposed to high temperatures. Likewise, *noveboracensis* that were initially subjected to low temperature had a lower level of food consumption at high temperature, after 30 days at the intermediate temperature, than individuals of the same species initially exposed to high temperature. The opposite was true

for *bairdi* which had a slightly higher level of food consumption after previous exposure to low temperature.

The explanation for the higher rate of food consumption, at the same low temperature, of animals having a warm thermal history in contrast to animals with a cool thermal history may lie in a decreased insulative efficiency of the pelage. It was found (Sealander, 1951) that winter *noveboracensis* acclimated for 30 days at high temperatures (29.5°–32.5°C.) underwent a significant decrease in pelage density. Likewise, laboratory-reared *bairdi* acclimated at high temperatures for

TABLE 4.—*Comparison of food consumption of two groups of P. m. bairdi in relation to air temperature, previous thermal experience, and duration of exposure to a given range of temperature*

	AVERAGE DRY WEIGHT OF FOOD CONSUMED PER DAY (GRAMS)			AVERAGE CALORIC INTAKE PER GRAM PER DAY		
	Group I†					
Average temperature, °C.*	8.5 (65.8)	20.5 (44.0)	30.5 (30.5)	8.5 (65.8)	20.5 (44.0)	30.5 (30.5)
0–10 Days	5.49	4.07	2.93	1.318	0.967	0.728
10–20 Days	5.22	3.39	2.20	1.257	0.785	0.564
20–30 Days	5.57	3.45	2.32	1.301	0.799	0.604
0–30 Days	5.42	3.63	2.48	1.300	0.851	0.631
	Group II‡					
Average temperature, °C.*	30.5 (30.1)	20.5 (44.0)	8.5 (66.4)	30.5 (30.1)	20.5 (44.0)	8.5 (66.4)
0–10 Days	2.45	3.20	5.82	0.603	0.727	1.269
10–20 Days	2.16	3.58	6.24	0.511	0.807	1.321
20–30 Days	2.24	3.62	6.32	0.521	0.826	1.330
0–30 Days	2.28	3.47	6.13	0.538	0.788	1.315

* Mean relative humidity, per cent, in parentheses.

† Four animals, measurement started in 6.0–10.5°C. range.

‡ Four animals, measurement started in 29.5–32.5°C. range.

the same length of time had a significantly less dense pelage than animals acclimated at low temperatures. It appears that animals initially subjected to high temperature compensate for a decreased insulative efficiency by an increased rate of food consumption (Fig. 1). On the other hand, the slight decline in food consumption at high temperatures of *noveboracensis* initially subjected to low temperature may have been due to a gradual increase in pelage density. Summer animals acclimated for 30 days at low temperature underwent an increase in pelage density which did not, however, reach a level of statistical significance. Better insulative efficiency of the pelage would also account for the observed decrease in rate of food consumption at low temperatures of these animals over those initially subjected to high temperatures.

Measurements of food consumption by different investigators for the same

species at equivalent temperatures may not always be comparable because of differences in the previous thermal history of the animals and the period of time allowed the animal to adjust its rate of food consumption to the surrounding temperature before measuring food consumption. Chew (1948) found that the average food consumption of 5 *noveboracensis* at 28°C. was 2.76 grams per day, while the average daily food consumption of an unstated number of *noveboracensis* at 28°C. in dry air was determined by Dice (1922) to be 2.78 grams. The average food consumption at 30.5°C. of six *noveboracensis* having a previously

TABLE 5.—*Comparison of food consumption of two groups of P. m. austerus in relation to air temperature, previous thermal experience, and duration of exposure to a given range of temperature*

	AVERAGE DRY WEIGHT OF FOOD CONSUMED PER DAY (GRAMS)		AVERAGE CALORIC INTAKE PER GRAM PER DAY	
	Group I**			
Average temperature, °C.*	8.5 (66.7)	20.5 (43.8)	8.5 (66.7)	20.5 (43.8)
0–10 Days	2.99	2.48	0.751	0.580
10–20 Days	3.07	2.27	0.739	0.537
20–30 Days	2.80	2.03	0.678	0.483
0–30 Days	2.95	2.35	0.722	0.555
	Group II***			
Average temperature, °C.*	30.5 (29.3)	20.5 (43.8)	30.5 (29.3)	20.5 (43.8)
0–10 Days	2.14	2.23	0.570	0.559
10–20 Days	1.59	2.33	0.410	0.585
20–30 Days	1.52	2.27	0.459	0.571
0–30 Days	1.75	2.29	0.447	0.567

* Mean relative humidity, per cent, in parentheses.
** Four animals, measurement started in 6.0–10.5°C. range.
*** Three animals, measurement started in 29.5–32.5°C. range.

cool thermal history was found in this study to be 2.79 ± .04 grams per day over a 30-day period. The measurements in these three studies compare very closely. However, another group of six *noveboracensis* previously acclimated at 20–24°C. for 4–5 weeks had an average daily food consumption of 2.94 ± .09 grams at 30.5°C. over a 30-day period.

The average caloric intake per gram body weight per day for *noveboracensis* and *bairdi* was higher in this study at 20.5° and 30.5° than at the equivalent temperatures of 21° and 28° in the study of Dice (1922). Possibly an animal may need a certain amount of bulk in its diet at different temperatures, regardless of the caloric content of the food. This may be governed by such factors as increases and decreases in the emptying rate of the stomach at different temperatures (Sleeth and Van Liere, 1937). The same quantity of food ingested, if the caloric

content of the two different diets differs, might then yield different caloric values per gram body weight, providing that the weight of the animals is approximately the same. The caloric value of the food used by Dice was about 4.0 Calories per gram as compared with a value of 4.26 Calories per gram for that used in this study. The lower caloric intakes per gram body weight found by Dice seem to be due largely to the lower caloric value of the diet which he used. If it is assumed that Dice's animals had the same average weight, namely 24 grams, as in this study, the difference in caloric intake per gram body weight may be explained entirely upon the difference in caloric content of the respective diets. Differences in weight are probably responsible for small differences which can not be explained on the above basis.

Body weight changes of *noveboracensis* showed little consistent relationship to food consumption. About half of the animals in groups I and II showed an inverse correlation of body weight with temperature. The remainder showed a more or less positive correlation. Group averages (Fig. 2) indicate an inverse correlation with air temperature. Seven of the twelve animals in the experiment were definitely above average weight at the start of the experiment. Pregnancy accounted for the increased weight of two animals in group I and one in group II during the first 14–22 days of exposure at high and low temperatures. Weights of pregnant females were excluded from the group averages.

A more definite inverse correlation of weight gain with food consumption and air temperature was shown by *bairdi* (Fig. 2). This is best illustrated by the weight changes during the final 30-day periods of exposure at high and low temperatures.

No consistent relationship between weight gain or loss and either air temperature or food consumption was evident for *austerus*.

As no quantitative measurement of activity was made, the influence of this factor upon body weight and food consumption at different temperatures cannot be properly evaluated. Brobeck (1945) found a negative correlation between weight change and activity in the albino rat when food intake and environmental temperature were constant. Increasing the food intake also increased weight gain when activity and temperature were constant, and weight gain was greater at 86°F. than 70°F. when food intake and activity did not vary.

Increases and decreases in rate of food consumption in response to changes in environmental temperature may be considered as immediate short-term adjustments enabling the animal to achieve a limited sort of acclimation to altered enviromental temperature before the slower adjustments! n pelage, amount of reserve fat, and metabolic rate are completed. The small animals considered here adjusted their rate of food consumption more rapidly to lowered than to raised temperature. The reasons for this are not readily apparent, although there may have been a proportionally greater increase in appetite induced by cold than a decrease occasioned by heat. Complete acclimation can not be achieved by adjustment in the rate of food consumption alone, particularly to low temperature, since the rate of food intake is obviously limited by digestive capacity as well as by the efficiency of the digestive processes. Changes in metabolism resulting

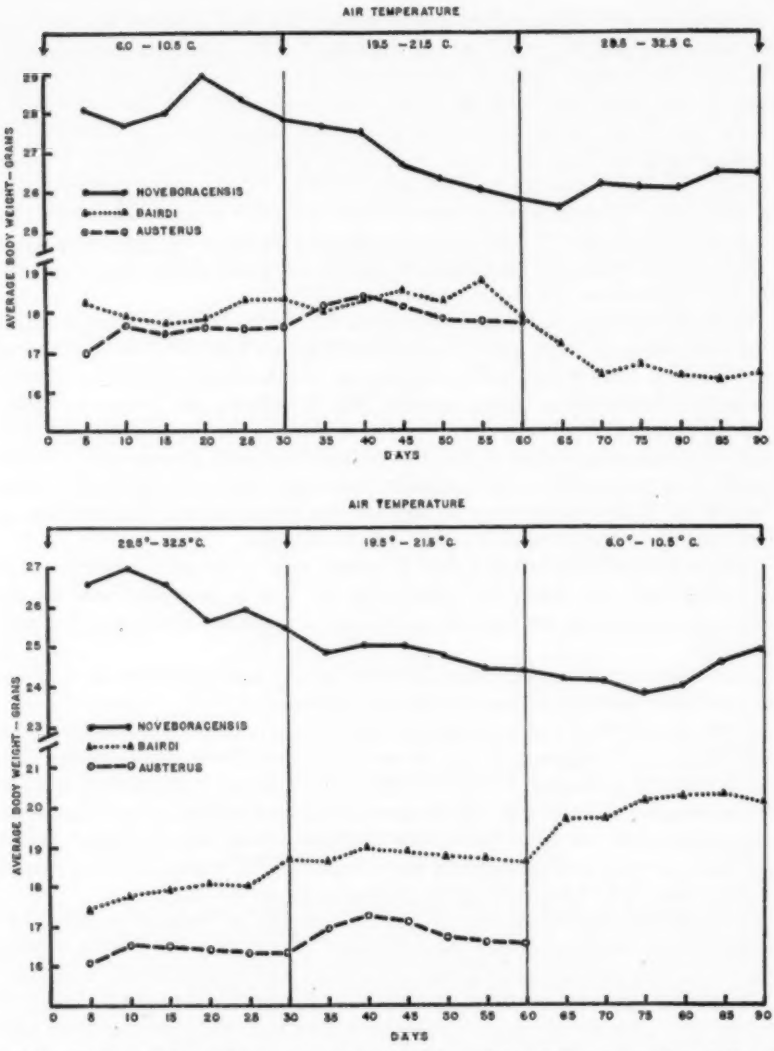

FIG. 2.—Comparison of group averages of body weight of *Peromyscus* in relation to periodically raised air temperature, *upper*, and periodically lowered air temperature, *lower*.

from the interactions of different hormones and changes in the insulative properties of the pelage and subcutaneous fat deposits must accompany changes in the rate of food consumption to keep the latter within reasonable limits. Thus, the

animal may adjust its rate of food intake to compensate for normal daily or weekly fluctuations in environmental temperature, but must rely upon other adjustments to achieve acclimation to prolonged seasonal variations in temperature.

Summary.—Food consumption of *Peromyscus l. noveboracensis*, *Peromyscus m. bairdi*, and *Peromyscus m. austerus* was found to vary inversely with air temperature. At equivalent temperatures *noveboracensis* ate more food per day than did *bairdi* or *austerus*. The caloric intake of *bairdi*, per gram body weight per day, was greater at all air temperatures than that of *noveboracensis*, while that of *austerus* was lower at all temperatures than either of the other two.

In relation to sudden lowering or raising of air temperature, all of the mice underwent an initial period of adjustment in rate of food consumption. This adjustment was most rapid at low temperatures, taking from 8-12 days. Adjustment to high temperature took place in about 15 days.

Animals with a previously warm thermal history had higher rates of food consumption after about 15 days at intermediate and low temperatures than did animals with a cool thermal history. Animals with a warm thermal history had a thinner pelage and apparently compensated for their reduced insulative efficiency at low temperatures by increasing their rate of heat production through increased food consumption. The reciprocal relationship at high temperatures was observed for *noveboracensis*, but not for *bairdi* or *austerus*.

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Department of Zoology, University of Arkansas, Fayetteville, Arkansas. Received May 28, 1951.

GONADOTROPHIN-INDUCED OVULATION IN MINK

BY JOHN HAMMOND, JR.

Our knowledge of reproduction in mink has been reviewed, and augmented, by Hansson (Alb. Bonniers Boktryckeri, Stockholm, 1947). There is a short breeding season in spring and it is possible to obtain only one litter a year. Ovulation is not spontaneous; there may be a variable period of delayed implantation, and during this time a mated female may mate and ovulate again.

It would greatly lower production costs if it were possible to obtain more than one litter annually. The experiments described here formed the first part of an investigation directed towards that end. Pregnant mare serum gonadotrophin (PMS) was used as a follicle growth stimulating agent. It was necessary to perform most of the experiments during the pelting season, when sexually active males were not available, so chorionic gonadotrophin (PU) was given to induce ovulation.

A few animals, anoestrous owing to previous artificial light treatment, and a few others that had failed to mate naturally, were given gonadotrophin towards the end of the natural season and allowed to mate. The other treated animals were killed and a search was made for tubal ova; representative ovaries were serially sectioned.

MATERIAL AND METHODS

The PMS and PU used were 'Antex' and 'A.P.L.' supplied by Ayerst, McKenna, and Harrison. Injections were always given subcutaneously, in the region of the axilla, in a volume of 0.5 cc. Another gonadotrophin used was a pituitary extract admixed with a water-soluble wax. This was given as pellet implants. The latter did not give satisfactory results, and animals so treated were useful only as controls.

The mink were on a farm at some distance from the laboratory. Killing and dissection of treated animals was done on the farm. The mink were killed with cyanide, pelted after the carcasses had cooled, and the ovaries and uterus then (1–6 hours later) were dissected and examined.

The experiments involving slaughter had to be completed within a brief period. Determination of the results of treatment by inspection of the fresh ovary, and

flushing for ova, was therefore attempted. This was done only on one side; the other was preserved for the more tedious and time-consuming method of serial sectioning and histological examination, if necessary, to confirm, or correct and extend, what was seen in the fresh material.

Vaginal smears were taken from the anterior end of the vagina with a moist cotton swab held on fine forceps. At killing, one ovary, with its accompanying tube and tip of uterine horn, was fixed as soon as the animal was opened. The other ovary was dissected free of the capsule and examined under the binocular microscope. Its tube was flushed out with 0.9 per cent NaCL solution and the flushings were searched for ova.

The technique of flushing was essentially that used previously (Hammond, Nature, 163: 28, 1949) in the mouse. Usually this was quite easily performed, though sometimes the tube had to be flushed as two to four separate segments. At first the ovarian capsule was cut away without disturbing the secondary coiling of the tube. Later it was found better not to remove the entire capsule; only that side attached to the hilum of the ovary was cut away. The pipette was inserted into the uterine end of the tube.

RESULTS AND DISCUSSION

There were two main experiments in which treated animals were slaughtered during the pelting season. The results from these are given first. The first, which will be referred to as the November experiment, was concerned with finding a suitable dose of follicle-stimulating agent, and testing the capacity of PU to cause ovulation of the artifically-developed follicles. In the second (December) experiment, the effect of administering a chosen total dose of PMS in different sub-doses was investigated.

November experiment; initial results.—The ultimate object was to obtain a treatment whereby anoestrous mink could be made oestrous, caused to mate and ovulate, and their ova be fertilized and able to develop following treatment. Since proestrus seems normally to be prolonged it was considered desirable that during treatment some time be allowed for proper development of the reproductive tract under the influence of the stimulated ovaries. On the other hand a long period of treatment is, practically, inconvenient.

Nine days was chosen as the interval between first administration of PMS and the time at which induction of ovulation was attempted. Three total doses of PMS were used—50, 100, and 200 i.u.—given to animals prefixed, respectively, D, F, and G. The total dose was given in two installments, 40 per cent initially, 60 per cent four days later. The dose of PU employed (200 i.u.) was known to be effective in the oestrous ferret. It is very possibly much larger than is needed.

Most of the females available for experiment had been born that year. The smaller number of adults were possibly unsuitable material since they had been sterile or of low fertility the previous season; however, the young and older animals might have responded differently. Accordingly, both were treated; one adult for each two young. In each group nos. 1–8 were young and 9–12 were adult females.

TABLE 1.—*Macroscopic appearance of right ovary, and ova flushed from right tube, of mink treated in November with PMS*

TREATMENT INTERVAL, INJECTION TO KILLING	NO.	GROUP AND DOSAGE											
		D, 20 + 30 i.u.				F, 40 + 60 i.u.				G, 80 + 120 i.u.			
		Ovary			Ova Recovered	Ovary			Ova Recovered	Ovary			Ova Recovered
		Weight (mg.)	CL	Follicles		Weight (mg.)	CL	Follicles		Weight (mg.)	CL	Follicles	
9 days, no PU	7	52	1	2	—*	36	1	—	—*	77	16	5	—
	8	30	—	—	—*	44	1	—	—	54	—	5	—
	12	104	6	2	3 C	38	—	5	2 F, no C	56	—	6	6 C
12 days, no PU	1	30	—	—	—	36	—	—	6 F	47	2	2	—
	2	8	—	—	NW	50	2	4	5 F	27	—	4	—
	9	66	1	7	1 F	9	—	—	NW	43	—	3	—
12 days, PU 3 days before slaughter	3	45	—	7	2 F, no C	89	3	2	3 CP, 4 FP, 5 F	69	3	6	1, 7 F
	4	51	5	3	2 CF	32	4	4	6 CP, 6 FP	100	3	2	2 CP, 1 F
	5	56	—	3	1 F	52	2	2	3 C, no P	66	6	—	10 P, 2 FP
	6	36	2	—	1	47	6	5	6 CP, 2 CPF, 1 F	44	—	2	—
	10	40	3	4	No tube	140	16	—	8 F	20	—	—	—
	11	94	—	4	5 F, no C	19	—	—	—	64	2	3	1 C

Symbols: *, difficulty in flushing; C, with corona; P, in gelatinous plug; NW, not flushed; F, fragmented.

Three in each group (nos. 7, 8, and 12) were examined 9 days after the first administration of PMS, and three each (nos. 1, 2 and 9) 12 days later Six (3–6 and 10, 11) of each group were given PU at 9 days, and killed 12 days after their first dose of PMS. Ovulation normally (Hansson, *loc. cit.*) is 36 hours after mating and tubal passage of ova occupies six days; three days after PU administration seemed an appropriate time to examine for induced ovulation.

There were 36 animals (and a further 36 given pituitary) used in this experiment, plus two old and four young controls. The work of examining ovaries and searching for ova was shared between two observers, and the findings are presented in Table 1.

In no animal was there pronounced vulval swelling; however, swelling is not necessarily well marked in oestrous mink. The vaginal smears of all PMS-treated mink, taken at slaughter, were of pro-oestrous or oestrous type; in general the response ran parallel to the dosage.

The animals given the highest pituitary dose showed a very definite vaginal smear response—about equivalent to that produced by 100 i.u. PMS. Only three ova were recovered from pituitary-treated females; in only one ovary was a corpus luteum (C.L.) seen. This was an adult female given PU (and the lowest pituitary dose). The other two females from which ova were recovered were both adults, one killed 9 and the other 12 days after first treatment; neither had been given PU.

The results with PMS-treated females, following flushing of the right fallopian tube, examination of the fresh, and weighing of the (fixed) right ovary, are given in Table 1. Comment needs to be made on these data.

The ovaries were preserved in Kaiserling's fixative, in the hope that hormone effects could later be studied at leisure, and in the light of experience gained, upon the ovaries, without the need to resort to serial sectioning. In fact the appearances of the fresh ovaries were not sufficiently preserved by this fixative.

After a study of sections, and more experience with fresh ovaries, it is clear that the lack of correlation between number of C. L. seen and of ova recovered is due to: (1) some recent corpora, being refilled with fluid, were probably recorded as follicles; (2) in many animals there were C.L. of different ages; the older were not conspicuous, and probably usually not recorded; (3) some corpora had ova retained within them (but these if recently formed were probably noted as follicles, or, if older, overlooked). The efficier cy of tubal recovery was probably quite good, but it is not certain that all ova shed remained in the tube.

The animals were examined in random order and the findings only later related to treatment given. Only after a number of mink had been dissected was it realised that the ova in each animal were not all of the same age. So a full record was not kept of the appearance of all recovered ova. Unless, in Table 1, a corona radiata, ovulation plug, or fragmentation are specifically referred to, against a particular animal, the lack of these features should not be assumed when they are not noted.

The ova exhibited a variety of appearances. Some with a substantial corona were free in the tube, others were embedded in a gelatinous plug; some without

corona were not greatly shrunken, others were shrunken and dark, often fragmented. These latter were usually free, but sometimes in a plug with other ova; perhaps they got embroiled in the plug when the tube was flushed.

The data on ova recovered by tubal flushing may be summarized. At nine days (5 after the second injection of PMS) ova were found in one of three in each group. In two cases the ova had coronae, in the third not. These were all from old females. At 12 days (8 days after the second PMS), in females given no PU, ova, all fragmented, were recovered in groups D and F. They were not, however, recovered from all these females or from any in group G (with the highest PMS dosage). At 12 days, when PU had been given three days earlier, ova were recovered from nearly all animals, but all ova were not in the same condition. Evidently some were from ovulations induced by the PMS, and others had been shed following the administration of PU. The exceptional cases were a young female (G.6, with an ovary rather smaller than others in its sub-group) and three adults. One of these latter (D.10) had almost certainly ovulated, but as the right fallopian tube and uterus were lacking the ova could not be found. In the other two (F.11, G.10) the dissected ovaries were small and appeared inactive, both had adhesions to the capsules.

The dissected ovary of another adult (F.9) was also very small, and adhesions were noted in some adults treated with pituitary. Accordingly (Table 2), specimen young females only (1, 3, 5, and 7 of each group) were taken, together with one adult and two young controls, for serial sectioning of the undissected and unflushed left ovary and tube. In addition the left ovary and tube of the anomalous G.6, and the dissected ovaries of F.9, F.11, and G.10 were also serially sectioned. The results of this examination are presented later. A second experiment was immediately started.

December experiment.—There were three groups of six, young females. All were given the same amount, 125 i.u. of PMS. From the results of the previous experiment this seemed an adequate dose. All were given PU (again 200 i.u. subcutaneously) three days before killing. In the hope of getting better oestrous responses in smear and vulva the interval from first administration of PMS until PU injection was increased from 9 to 11 days.

Three ways of giving the PMS were tried, in the hope of obviating the induction of ovulation by this substance. To group R the complete dose was given at once. To group S, a dose of 50 i.u. was given first and the remaining 60 per cent was given five days later. Group T had 45 i.u. initially, with 20 i.u. two, four, six, and eight days later (these 20 i.u. injections were given by the mink farmer).

Vaginal smears were taken at the time of PU injection and again at killing. Notes on vulval swelling were made at the same times. At killing the November procedure was followed, except that the uterus also was flushed (except the tip of the left horn).

Indications of vulval swelling were seen in all animals. It was in no case very marked and was less than that encountered, on the average, in natural oestrus. There was no obvious difference between groups R, S, and T.

Smears taken at the time of PU injection could be considered oestrous in all but R.1, R.5, and S.1. That is to say, they consisted almost entirely of plate-like epithelial cells, mostly with ragged edges and pyknotic nuclei. Leucocytes were present in appreciable numbers only in smears from R.1 and R.5. Three days later, at killing, R.1 and R.6, and all of groups S and T, had oestrous smears. Smears of R.2–5 were mainly of plate-like cells, but more of these had smooth edges and large and lighter-staining nuclei; from R.3 and R.4 there were numbers of leucocytes.

The data on ovulation points seen and ova recovered are listed in Table 3. Serial sections, in this experiment of the dissected ovary, were made from sample cases and the table also gives a summary of the findings.

There was cause to place reliance upon the observations made of ovulation points in the fresh ovary. The numbers of C.L. observed and of tubal ova recovered tallied well; except in S.4 (9 C.L., 10 ova) number of ova was less than or the same as number of C.L., and ovum recovery was apparently 85 per cent. In fact, in the sample ovaries sectioned, the ovulation points observed fresh do tally with recently formed C.L. in the sections, but older C.L. were overlooked in the fresh ovaries. It would seem, from the variation in appearance of the ova recovered, that some were derived from these older C.L. This was not realised until after the old C.L. had been found on sectioning. The results known after dissection were as follows: ovulation had not been consistently induced by PU in groups R or T; in only two of each group were ovulations seen, though in a third animal of group T a degenerate ovum was found in the uterus, apparently without a C.L. from which it could have originated. It was possible that ovulation had occurred in the left ovary of others, but the total number of ovulations was unlikely to be satisfactory.

C.L. were seen, and tubal ova recovered, from all of group S and the number of ovulations was like that seen following normal mating. In two of the six examples of group S, ova were found also in the uterus—two in the right horn of S.6, one in the left of S.2.

It may be pointed out that nothing is known of the fate of unfertilized ova shed after normal mating. Hansson (*loc. cit.*) makes no mention of an ovulation plug; but he states that after ovulation "as a rule the egg is freed from the corona radiata already in the infundibulum. . . . The passage of the egg through the first part of the tube is very rapid. . .48 hours after the mating of mink, i.e. 12 hours after ovulation, the eggs were found in the middle part of the tube," and he illustrates one such ovum which is apparently devoid of any corona. If PU induces ovulation after the same interval as does mating at oestrus, tubal ova in group S should have been 36 hours old, and the absence of a corona from some of them was by no means a certain indication that they were more than 36 hours old. Fragmentation of three of the 22 ova was more puzzling, but perhaps attributable to a defect before ovulation.

Serial sections showed that the second dose of PMS had consistently induced ovulation. Alternate animals of this group (S.2, 4, 6) were examined by sectioning to check the (mistaken) supposition that the minor modification of treatment

from that given in November had averted the ovulating effect of the PMS. Treatments of groups R and T were evidently of no commercial use so two only (nos. 2, 5) were taken for sectioning, one in which ovulation was known to have been induced by PU and one in which it was not. Meanwhile experiments in the breeding season were based upon the treatment given animals of Group S.

March experiments.—By March 14, 93 per cent of untreated females at the farm had mated. None of 15 females previously given light treatment (Hammond, unpublished experiments) had then oestrous smears. Two that had mated were distinguished from the other 13 by the amount of mucus in the vaginal contents. One of these two produced young, the other is not known to have done so. The smears of the remaining 13 were of a typically anoestrous nature, and it is unlikely that they were pseudopregnant.

These 13 were treated with PMS in the same way as group S; after the second PMS injection they were tried with males, and eight mated (2 five days, 2 six days, 3 eight days, and one nine days after the second dose of PMS). Alternate females of these eight were given 200 i.u. PU at mating.

These females had failed to mate earlier in March, but were treated and subsequently mated on the farm, and the farmer reported that, though the males were keen, the females seemed not truly oestrous. He added that they behaved in much the same fashion as some unmated females to which he had administered stilbestrol (in very heavy dosage) in an earlier year. Those females had mated, but produced no young.

One only, of the eight females mated after PMS treatment, produced young. This one had mated five days after the second injection, and had been given PU.

The other females available for experiment in March were twelve that had been kept under normal conditions, but which had failed to mate until the breeding season was nearly over. There can be confidence in the farmer's assertion that these females had not mated, but it is not so certain that they had not ovulated. According to Hansson the mink vaginal smear remains oestrous after ovulation while the corpora lutea remain in the resting phase, and afterwards reverts to the anoestrous type. Smears were taken towards the end of March from these twelve unmated females. Four had anoestrous smears and were given, like group S, 50 i.u. PMS with 75 i.u. five days later. Four days after this they were again tried with males. One each mated four, five, and seven days after the second PMS injection, and one failed to mate. None produced young.

Three had smears neither oestrous nor typically anoestrous in character. There were few or no plate-like cells, but there were more, and larger, epithelial cells than in anoestrus; the leucocytes were mainly not degenerate; among the epithelial cells were some with mucous (?) vacuoles. These latter cells seem to correspond, in mink smears, to the large pale-staining round cells found in the ferret (Hamilton & Gould, Trans. Royal Soc. Edinburgh, 60: 87, 1940) in pro-oestrus and after ovulation.

Five had smears of oestrous type. Artificial insemination (by Dr. M. C. Chang)

and injection of 200 i.u. PU, was performed on these five, on two of the three with transitional smears, four days after they had been given 50 i.u. PMS (the smears of these two at the time of insemination remained of the same character), and on the five unmated, light-treated females, eight days after their second PMS treatment (when they had appreciable vulval swelling and their vaginal smears were of oestrous type).

The third female with transitional smear was killed for examination, without treatment, as was one of the five with oestrous smears, three days after PU injection. PU had induced ovulation in this last mentioned female; four ova, all with substantial coronae, were recovered; two of them were serially sectioned, but no sperm were found.

None of the others produced young. Successful artifical insemination of mink and ferrets has not been described, so this negative result need not be ascribed to failure of the PU to induce ovulation. Nor necessarily need the insemination technique have been inadequate, since a failure to obtain fertilization and implantation when ovulation is induced in the presence of an active C.L. is a general experience, and it is likely that most of the treated mink did have active luteal tissue already present at the time of insemination.

That there were corpora lutea already formed before mating in those females given PMS is probable from the results of the experiments in November and December. That the C.L. were functional is probable, from the time of year. It may be remarked that what was noted of the mating behaviour of these females is very like what may be observed in sheep and cattle injected with oestrogen in the presence of an active C.L.

That there were active C.L. in those unmated females with transitional and oestrous smears at the time of insemination is likely, since they were found in the sample females killed. The activity of these C.L. may be assumed from their histological appearances and those of the associated uterine epithelia.

HISTOLOGICAL OBSERVATIONS

The following material was studied: the ovaries of various possibly abnormal adult females (F.9, F.11, G.10) and the undissected ovary and tube of one young female (G.6) of the November experiment; the undissected ovary and tube of alternate young females of this experiment (D, F, G, 1,3,5,7), and of controls; the dissected ovaries of seven animals of the December experiment (R and T, 2,5; S, 2,4,6); and sample ovaries and uteri of two unmated females killed in March—one entirely untreated, which had a 'transitional' type of vaginal smear, and one with an oestrous smear three days after being given PU and inseminated. The serial sections were cut at 8–10 μ; Haematoxylin and Van Gieson were the stains employed.

Ovary.—Hansson has described the histology of the mink ovary and the developmental phases of the corpus luteum. The bulk of the ovary is made up of interstitial cells, rather like those of the rabbit, arranged in cords along loops of capillaries. The interstitial cells are presumably derived from the theca of

degenerate antral follicles. With few exceptions (to be mentioned shortly) all the ovaries examined contained numbers of unresorbed, usually crumpled, zonae pellucidae with interstitial cells arranged more or less radially about them.

Primordial follicles were abundant in all the ovaries. In the adult control ovary examined there were only three follicles with antra; unresorbed zonae in the cortex were small and few in number. Follicles with antra were fairly

TABLE 2.—*Corpora lutea and ovulated ova, from left ovary and tube, from serial sections; November experiment*

DAYS BETWEEN FIRST INJECTION AND KILLING	NO. OF MINK	OLD CL		YOUNG CL		OVA RECOVERED	
		Without Retained Ova	With Retained Ova	Without Retained Ova	With Retained Ova	Number and State	Position
9 days	D7	2	1	—	—	—	—
	F7	4	2	—	—	—	—
	G7	34	5	—	—	4 C, 1 no C	fimbria and capsule
12 days, no PU	D1	—	—	—	—	—	—
	F1	22	2	—	—	4 F no C 5 F no C	½ down tube in uterus
	G1	24	24	—	—	—	—
12 days, PU 3 days before killing	D3	7	1	—	5?	1 F no C, 1 F tC 4 tC	¼ down tube Tubal junction and uterus
	D5	16	—	—	1	3 tC, 1 F tC	½ down tube
	F3	33	5	—	1	1 FC, 9 tC, 1 no C	½ down tube
	F5	9	1	2	1	1 tC, 1 no C 2 C, 1 tC	½ down tube ¾ down tube
	G3	14	—	10	6	8 C, 2 tC, 6 no C, 4 F no C	all in fimbria and top ½ of tube
	G5	11	19	10	4	7 C, 1 FC	fimbria
	G6	2	15	9	15	3 tC, 4 no C	all in top ½ of tube

Symbols: C, with corona radiata; No C, no corona; tC, with portions of corona remaining; F, fragmented; ?, follicles possibly luteinising.

numerous (10–15) in one young control; in the other there was only one such follicle in one ovary, but several in the other.

The seemingly abnormal small right ovaries of F.9, F.11, and G.10 all had adhesions between ovary and capsule. In the cortex of G.10 there were two fibrous patches. Neither this ovary nor those of F.9 or F.11 contained follicles with antra; further, there were no unresorbed zonae in any of these three ovaries. These were barren females; the absence of unresorbed zonea suggests that there had been no antral follicles for an appreciable period, so it is not surprising that gonadotrophin treatment evoked no ovulation in these ovaries.

The left ovary and tube of G.6 was sectioned, as (Table 1) no ova were recovered from the right side. The condition (Table 2) of this ovary was very similar to that of the left ovaries of G.3 and 5, treated in the same way. It seems safe to dismiss the failure to recover ova from the right side as due to defective technique.

The findings in the serially sectioned sample ovaries of the November experiment are given in Table 2. The corpora lutea in the treated mink fell into two quite distinct classes, described in the table as 'old' or 'young.' Many of both types seem to have been formed without rupture of the follicle; this is true certainly of the 'young' ones, in the 'old' it was not easy to detect the ovulation points of any. At all events, some corpora of both types had ova retained within them.

'Young' C.L. were present only in those given PU (72 hours before killing). Since ovulation normally occurs 36 hours after mating, it is unlikely that they were more than 36 hours old. From their appearance they are unlikely to be less than 24 hours old. The luteal cells were enlarged, larger than in the 'old' corpora, and their nuclei vesicular, quite unlike the heavily-staining nuclei shown by Hansson (*loc. cit.*, fig. 52 [fig. 50 in text]) of the C.L. three hours after ovulation, at which stage he says the follicle cavity is nearly obliterated. Most of these young corpora had a considerable cavity, whether or not there was a rupture point. A system of blood vessels was established, but the central cavity was not outlined by fibrous tissue.

'Old' corpora corresponded to the description given by Hansson for the inactive phase; the cells were smaller, both in nuclear and cytoplasmic volume; there were more connective tissue and vascular elements present, but less blood within the vessels; the centre was filled (or cavity lined) with collagen fibres. A small cavity was generally present in corpora with a retained ovum. Except in G.7, these old corpora were all very much of the same appearance, but this does not necessarily indicate that they were formed all at the same time in the different animals, or even in one animal.

It is implied in a statement of Hansson's (*loc. cit.*, p. 53. "Ten females had mated twice, with at least 8 days between matings, but two of them had not such a large number of corpora lutea in the ovaries that it could be assumed with certainty that they had ovulated twice.") that when there are naturally two lots of ovulations, the corpora of the first do not regress when those from the second have formed. It would, therefore, probably be rather hard to distinguish corpora of different ages when both have had time to regress to the 'resting-phase' condition.

In G.7, the 'old' corpora may have been more recently formed than those in other ovaries. The luteal cells were large, and there was collagen in the centre of the corpora, but less than in those of other ovaries.

In all sample ovaries of the November experiment, except that of D.1 (with the lowest PMS dose), there were old C.L. Young C.L. were present only in those given PU; and were present in all of those sectioned, except D.3, again an animal given the lowest PMS dose. In Table 2 there are listed against this

TABLE 3.—*Corpora lutea detected in fresh ovaries and in serial sections (right ovary), and ova recovered from uterus and right tube; December experiment*

NUMBER	GROUP R			GROUP S			GROUP T		
	CL in Serial Sections	Examined Fresh		CL in Serial Sections	Examined Fresh		CL in Serial Sections	Examined Fresh	
		CL Seen	Tubal Ova Recovered		CL Seen	Tubal Ova Recovered		CL Seen	Tubal Ova Recovered
1	†	—	—	†	2	1 C 1 F, No C	†	1	—
2	No old 3 + 0 young*	2	2 CP	3 + 0 old 4 + 2 young	5	3, No C, P[1]	3 + 0 old No young	—	—[3]
3	†	—	—	†	4	2 C 1 F, No C	†	—	—
4	†	—	—	2 + 1 old 10 + 0 young	9	6 CP, 2 C 2, No C	†	—	—
5	No corpora lutea	—	—	†	2	1 F, No C	No old 5 + 0 young	5	4 CP
6	†	1	1 C	2 + 2 old 3 + 1 young	3	3 CP[2]	†	—	—

Symbols: †, ovary not sectioned; *, 3 + 0 = 3 without retained ova, and none with retained ova; C, with corona radiata; F, fragmented; P, gelatinous plug.

No ova recovered from either horn of uterus, except as noted: [1] S2, 1 ovum, in a gelatinous mass, but without corona, in left horn; [2] T2, 1 fragmented ovum, no corona, from right horn; [3] S6, 2 unfragmented, but very dark ova, without corona, in right horn.

animal five doubtful young C.L. with retained ova; these bodies may have been degenerating follicles. The granulosa cells were not enlarged, but in one there was a thickening of the theca interna with blood vessels penetrating into the granulosa. In others there were free red cells among the granulosa, and in two of them capillary loops penetrated the granulosa and encircled the ovum. Corner (Princeton Univ. Press, p. 70, 1946) describes capillary penetration of the cumulus as typical of the sow follicle immediately before ovulation. It is thus possible that these follicles (of D.3) might have proceeded to luteinise.

In the sectioned ovaries of the December experiment, corpora lutea again were of the 'old' or 'young' types already described. The intervals between PMS injection and killing were longer, but those between PU and slaughter the same, as in the November experiment. It would, therefore, be expected that corpora formed after PMS would have reached the resting condition, and that those found after PU injection should be of the same age as in the November animals.

The numbers of old and young corpora found are listed in Table 3. It is to be noted that the ovaries sectioned had been examined fresh, and the results are a check on the reliability of those observations made on the fresh ovaries. It is justifiable to conclude that fresh ovulation points were rarely overlooked, and old corpora lutea consistently went undetected.

In Group S (50 + 75 i.u. PMS, separated by 5 days; with PU 6 days after the second PMS injection and 3 days before slaughter) it is evident that consistently ovulation and luteinisation followed one or both injections of PMS and again after the PU. In groups R and T ovulation (in the right ovary) followed PU in only two out of six in each group. In group R, where the PMS was given as a single injection of 125 i.u., there were no old C.L. in the two ovaries. In group T (45 i.u. PMS followed by 4 doses of 20 i.u. on alternate days thereafter) old C.L. were present in one of the two ovaries sectioned. It may be that there were old C.L. in the other ovaries, examined fresh but not sectioned (and in the left ovaries which have not been examined), however, ova to correspond were not found. Reference to the fate of ova is made later.

Reference has been made earlier to two females killed towards the end of the breeding season, both unmated, one untreated, one given PU and inseminated. An ovary of each was serially sectioned. The untreated female was one with a vaginal smear transitional between the oestrous and anoestrous types. The sectioned ovary contained 13 corpora in the 'active' stage (as after implantation). No ova were recovered from one tube flushed; there were no uterine swellings. The animal appears to have been pseudopregnant, ovulating as a result of excitement without copulation.

The other female killed had had an oestrous smear, when inseminated, and given PU (200 i.u.). It was killed three days after the PU. Four tubal ova rerecovered had complete coronae radiatae. There were young corpora (whose cells looked a little larger than those in animals of the winter experiments) in the ovary sectioned. There were also three abnormal corpora, clearly much older. Each had a fluid-filled cavity with a ring of luteal cells in the active phase, and they presumably originated by partial luteinisation of unruptured follicles at an attempted mating earlier in the season.

In those animals (D.3, most of groups R and T) in which PU did not induce ovulation it is likely that there were no large follicles. In the remainder, ovulation seems to have occurred after an interval not much different from that usual after copulation, an interval not incompatible with the fertilisation of ova by sperm inseminated at the time of injection. Whether such PMS-treated animals would mate, or, having mated, would release pituitary gonadotrophin sufficient to ovulate remains a matter for conjecture. Pituitary storage and release of ovulating hormone might be independent of the light-sensitive mechanism which regulates the natural season, or controlled by it directly, or normally be affected by it indirectly through ovarian secretions.

It appears probable that the conditions for induction of ovulation by PMS, as administered in these experiments, are much as those for PU. With a single injection (group R) ovulation was certainly not induced consistently; but it was with two spaced injections (groups D, E, F, S). One is justified in presuming that these ovulations were usually provoked by the second injection; but, as some control ovaries had large follicles, it is not unlikely that a single PMS

TABLE 4.—*Ratio of CL without and with trapped ova, formed after PMS and PU injection in groups of similarly treated animals*

	GROUP D	GROUP F	GROUP S	GROUP G	ALL FOUR GROUPS
PMS dosage (i.u.)	20 + 30	40 + 60	50 + 75	80 + 120	
"Old" CL (induced by PMS)	25:2	68:10	7:3	85:63	185: 78
"Young" CL (induced by PU, 200 i.u.)	0:1	2:2	17:3	29:25	48: 31
Total CL	25:3	70:12	24.6	114:88	233:109

injection would sometimes induce ovulation, and may have done so in some of these animals. Concerning the more exact timing of these PMS ovulations, it was hoped the position of recovered ova might help, but the studies made showed these hopes false.

All C.L. (except possibly in G.7) following PMS had reverted to the 'resting stage,' and they seemed mainly to have been provoked by the second injection given. They must then have ovulated (or otherwise passed through a stage leading to luteinisation) within a few days of that second injection. The dose at this injection was never more than the single injection given group R, and sometimes (group D) the total of both doses was less than half as great. Whether or not, in any given follicle, luteinisation followed PMS administration probably depended much more on the condition of the follicle at the time of injection than on the dose given (save perhaps in group T, with a small dose); the ovulations induced may well have been as closely spaced in time as those following PU.

Rowlands and Williams (Jour. Endocrin., 3: 310, 1942) induced ovulation readily with PMS in the hypophysectomised rat. Table 4 summarizes some of the data of Tables 2 and 3, comparing the luteinisation induced by PMS and PU administration.

The occurrence of luteinisation without release of the ovum may perhaps be

taken as an indication of abnormality of the stimulus applied. By this criterion, "follicle-stimulating" PMS is no more an abnormal stimulant than "luteinising" PU; in fact a smaller proportion of the PMS-induced C.L. have retained ova. As the PMS dose increases, though, the proportion of abnormal corpora (and total C.L./ovary) also increases, both when ovulation is induced by PMS and when it follows PU. In the latter case the comparison made is essentially between groups S and G, where the time intervals between injection are not the same; it may be that longer intervals of groups S favoured normal luteinisation. One is inclined to suppose that it was the condition of the follicle at the time of injection, rather than whether it was PMS or PU that was given, that determined whether ovulation would precede luteinisation.

In these experiments, C.L. formed after PMS were in the 'resting stage' at the time of killing, while those induced by PU were not yet fully formed. Presumably the C.L. formed after PU injection would in time also have passed into the resting-phase condition (except in that March-killed female which had also active luteal tissue at slaughter).

Assuming that full luteal function is dependent upon secretion of a pituitary luteotrophin, one may account for the occurrence of resting-phase C.L. at the start of the normal season as occurring *either* because an extrinsic factor (e.g. day-length) is not yet stimulating secretion of the principle *or* because the follicular activity of the breeding season (or its cause) depresses the production of this principle.

In the latter case the artificially induced C.L. should become functional upon elimination of the administered gonadotrophin, and one might have expected a difference in luteal cell-size between animals of group D (given 50 i.u. PMS) and those of group G (given 200 i.u.). That this was not noted is not conclusive, but inclines one to suppose that (without supplementary treatment) if mink were induced to ovulate in December, and their ova were fertilised, their C.L. would remain in a resting phase and the embryos unimplanted until March, if they survived so long.

After normal mating the ovulation plug must be soon broken up, and (Hansson, *loc. cit.*) within 12 hours the ovum is half way down the tube with its corona dispersed, though it does not reach the uterus until after about six days. The absence of sperm at ovulation in the experimental animals may be responsible for delayed dissipation of plug and corona (and so might lead to lengthened time of tubal passage). There evidently was delay (many ova with corona: G.7, Table 2, probably 3½ days post ovulation), but there are no data to decide whether this is attributable to lack of sperm or to some defect of tubal environment (or corona) caused by the hormone treatment.

Some ova still with corona were fragmented (Table 1; D.4, F.6, ova probably only 36 hours old); fragmentation may have been overlooked in others. It does not seem justifiable to conclude that a fragmented ovum must be derived from an 'old' C.L. Thus, in animals ovulating at more than one time it is difficult to decide the age of a recovered ovum, and hence whether it was being transported at a normal rate.

Certainly on the data given in Table 2 (position of ova in serially sectioned

fallopian tubes) there is evidence pointing towards abnormality of transport. For example, in G.7, five ova which must have been shed three days previously were found at the top of the tube; in F.5, two ova, shed one and one-half days, either were not found within the tube and capsule, or present further down the tube than two others shed probably five days earlier; and in G.3, 20 ova, not possibly all of the same age, were in the upper part of the tube. That ova enough to correspond to corpora were not found in the tube, that some in fact were seen in the uterus (which was not sectioned serially), is quite compatible with a normal rate of transport; for in most of the animals listed in Table 2, the interval between the second PMS injection and killing was eight days.

When it is considered how easily ova were flushed from the tubes it seems likely that they may have been displaced by the contractions of the tube in the fixative, hence, it is unwise to attach too much importance to the position of the ova in this fixed material. Recalling, however (F.3, F.4), the finding of fragmented ova without coronae in plugs, it does seem that ova may have been held at the top of the tube through failure of a plug to disperse.

Comparing, in groups F and G, the number of ovulations induced (left ovary, Table 2) with tubal ova recovered by flushing (right tube, Table 1), recovery is poorer in group G, which may indicate greater disturbance with the larger dose.

In animals of group S the possible intervals between ovulation and killing are 1½ days, 7½ days and 12½ days. With a normal rate of transport only ova from 'young' C.L. should be in the tube, and (S.2, S.4, S.6) the numerical correspondence is very good between young C.L. and ova flushed. The ova, however, are not all of the same appearance. Ova of those few animals (R.2, T.5) with only young C.L. (also of the females killed after PU in March) had all solid coronae. Of those few with only old ovulatory C.L. in one ovary (D.3, D.5, F.1, F.3, G.7, T.2), ova from G.7 had coronae, as did one ovum from F.3; the remainder had only traces, or none. It is probable that tubal ova without coronae from animals of group S were shed following a PMS injection, if 36 hours afterwards, they must have been 7½ days in the tube, in S.2 and S.4 the ova from 'old' C.L. were, then, all in the tube, and in S.6 were both in the uterus.

There was probably delay in tubal transport, not necessarily very great, and perhaps due not to the treatment as such, but to the absence of sperm at the time of ovulation.

SUMMARY

Pregnant mare serum gonadotrophin (except in some females with ovarian adhesions) was consistently effective in inducing follicle growth in anoestrous mink (at pelting time). One hundred international units is about a 'physiological' dose, in the sense of numbers of follicles matured and the response of the vaginal epithelium. Pregnancy urine gonadotrophin induced ovulation of such follicles. The pregnant mare serum also induced ovulation, and did so consistently when the dose was divided into two injections four or five days apart. The corpora formed went into the resting condition.

A method of combining treatment with PMS and PU such that ovulation was delayed until after the PU was given, yet occurred consistently, was not found (but few variants of treatment could be tried). Luteinisation without ovulation of some follicles was caused by both PMS and PU.

As males are not naturally active at this time, it was not practicable to test whether the treated females would mate, their ova become fertilised, be normally transported to the uterus, implant, and develop. These aspects are considered. Indications of delay in tubal transport may be due to absence of sperm. It seems probable that (assuming successful fertilization and transport) supplementary treatment would be required before implantation could occur (during the winter).

Of a few animals artifically made anoestrous, and treated during the normal season, some mated and one is reported to have produced young. This low fertility is not necessarily disappointing, as the treatment given may well have caused the formation of active luteal tissue (which is not likely to favour fertilization) before mating occurred.

Treatment, towards the end of the breeding season, of a few females that had failed to mate met no success. Two such animals examined had active luteal tissue (originating before any treatment was given, presumably from excitement without copulation). It seems improbable that gonadotrophin treatment can be generally useful with such animals at such a time of the season.

Special thanks are due to Dr. M. C. Chang for help with the dissection of the mink ovaries. Judy Pincus and Ann Merrill aided then, and later prepared the serial sections. Acknowledgment is gratefully made of the hospitality and help of the mink farmer and his family in these and other investigations. This investigation was supported by a grant from Benjamin Harrison Weiss, Inc.

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BATS OF THE MEXICAN STATE OF MORELOS

By William B. Davis and Robert J. Russell, Jr.

As part of a survey of the terrestrial vertebrates of Morelos undertaken by Davis and a group of his students in the Department of Wildlife Management, in cooperation with the Direccion Forestal y de Caza of Mexico, special efforts were made to determine the chiropteran fauna of the state. As a result, 195 specimens of 14 different species of bats were collected in the summers of 1949, 1950, and 1951. Perusal of the literature, coupled with specimens in our collection, reveals that a minimum of 20 kinds (species and subspecies) of bats occur in this small state. These are distributed by families as follows: Emballonuridae, 1; Phyllostomidae, 14; Desmodontidae, 1; Vespertilionidae, 2; Molossidae, 2. The paucity of species of common bats (Vespertilionidae) is indicative of the lack of influence the Nearctic fauna has on the total vertebrate fauna of the region.

For assistance in identification and for the loan of comparative materials, we express our sincere thanks to Dr. Walter W. Dalquest, Louisiana State University, and Mr. Stanley P. Young, U. S. Fish and Wildlife Service. Sr. Luis Macias and Sr. Bernardo Villa R., both with the Direccion Forestal y de Caza of Mexico, facilitated the field work in many ways. To them we express our deep appreciation.

ACCOUNTS OF SPECIES

Balantiopteryx plicata plicata Peters.—Fifty-nine specimens examined, as follows: Alpuyeca, 23; Puente de Ixtla, 3; Tecuman, 18; Amacuzac, 3; Axochiapan, 11; Temilpa, 1. Additional record (Sanborn, 1937): Cuernavaca.

This is the one of the most common bats in the arid lowlands of Morelos. It appears early in the evening, often before sundown. It can be recognized in flight by its small size and pipistrelle-like flight.

Martinez and Villa (1938) described as a distinct species *Balantiopteryx ochoterenae*, with material from Cuautla, Morelos. Unfortunately these specimens, including the type, were lost during Villa's absence from the Instituto de Biologia. The species *ochoterenae* was said to differ from *plicata* in paler color, the presence of long stiff hairs on the face above the eyes and at the corners of the mouth, and in other minor details. These characteristics have been found to agree with specimens of *B. plicata* from Guerrero. Therefore, we regard *Balantiopteryx ochoterenae* a synonym of *Balantiopteryx plicata plicata* as have Burt and Hooper (1941) and Dalquest, Frum, and Hall (1950).

A female collected June 8, 1951, at Amacuzac had one embryo which weighed 2.2 grams and measured 26 mm. from crown to rump. Other adult females captured in the same cave were not pregnant.

Chilonycteris personata Wagner.—Our three specimens, all from Alpuyeca, constitute the first record for Morelos and from the interior plateau region of Mexico. A previous record from Veracruz (Dalquest and Hall, 1949) increased the known range of this species north from Guatemala. These bats are probably associated with the tropical vegetation occurring along the lowland streams that traverse the arid plateau. Ours were shot in flight a short distance from such a habitat.

These bats emerge early in the evening like *Balantiopteryx* and associate with that genus in its evening flight. We were unable to distinguish the two kinds in the air.

All three specimens are bright fulvous above and below. A feature seemingly not mentioned in the literature is that the wing membranes attach high in the lumbar region producing a partial naked-back condition, but not carried to the extreme found in *Pteronotus*.

Chilonycteris rubiginosa mexicana (Miller).—Our two specimens were collected in a cave near Huajintlan, which they occupied with *Macrotus mexicanus* and *Leptonycteris nivalis*. Both of these specimens are in the brown color phase. Four specimens from an unknown locality in Morelos are in the U. S. National Museum (Rehn, 1904*c*).

Pteronotus davyi fulvus (Thomas).—One specimen, a female from Temilpa, seemingly is the first record of this bat from Morelos. Our specimen, in the brown color phase, was killed in flight over a marshy area.

Since Rehn's study of the genus (1904*b*), new records of distribution for this subspecies have accumulated which now permit a more detailed statement of its range. Specimens are now available from: *Jalisco*: no specific locality, 1 (AMNH). *Colima*: 7 mi. W and ½ mi. S Santiago, 38 (U.K.M.N.H.); Hacienda Magdalena, 1 (USNM); Plains of Colima, 1 (AMNH). *Michoacan*: Lake Chapala, 6 (AMNH); no specific locality, 1 (CNHM). *Morelos*: Temilpa, 1 (TCWC). *Guerrero*: Cave of Cacahuamilpa, 1 (MVZ), 3 (CNHM); Acapulco, 2 (BSC). *Oaxaca*: Santa Cruz Bay, 1 (UMMZ); Tehuantepec, 6 (USNM); Santa Efigenia, Tehuantepec, 2 (USNM). *Veracruz*: Achotal, 1 (CNHM); Mirador, 7 (USNM); San Andres Tuxtla, 4 (CNHM), 65 (UKMNH), 4 (BSC); South San Andres Tuxtla, 1 (BSC). *Campeche*: Apasote, 1 (BSC); La Tuxpena, Champoton, 2 (BSC). *Yucatan*: Chichen-Itza, 1 (CNHM).

Mormoops megalophylla senicula Rehn.—This species probably inhabits the semi-desert lowlands. Three specimens reported by Rehn (1902) from Morelos (exact locality unknown) are in the U. S. National Museum. We failed to encounter it.

Micronycteris megalotis mexicana Miller.—Martinez and Villa (1938) collected one specimen at Cuautla, in the desert-scrub lowlands. Seemingly this is the second record for Mexico, the other being from Plantinar, Jalisco, the type locality.

Macrotus mexicanus mexicanus Säussure.—Twenty-four specimens examined, as follows: Hacienda San Gabriel, 8; Puente de Ixtla, 10; Huajintlan, 6. Additional records: Cuautla and Cuernavaca (Rehn, 1904*a*); Las Estacas (Martinze and Villa, 1938).

Apparently this is the most common bat in the semi-desert lowlands of Morelos. We encountered hundreds of them inhabiting the tombs of an old monastery near Puente de Ixtla, and in a cave near Huajintlan it was the predominant species.

One of us, Russell, found one individual hanging from the ceiling of an open porch at Alpuyeca. An effort was made to catch it as it flew back and forth, but it escaped into the open. This bat inhabits the abodes of man as does *Tadarida*.

Glossophaga soricina leachi (Gray).—Twenty-three specimens examined, as follows: Alpuyeca, 20; Puente de Ixtla, 1; Hacienda San Gabriel, 2. Additional records (Miller, 1913): Cuernavaca and 20 mi. S Cuernavaca.

Measurements.—The averages and extremes in millimeters of 7 males from Alpuyeca are: total length, 64.3 (64–68); length of tail, 10.0 (10.0–10.0); hind foot. 10.1 (10–11); thumb, 6.7 (6.4–7.0); forearm, 35.7 (34.5–37.8); greatest length of skull, 21.5 (21.2–21.9); zygomatic breadth, 9.3 (9.0–9.5); maxillary tooth row, 7.2 (7.1–7.3); maxillary breadth at M^3, 5.5 (5.3–5.7). Of 12 females: total length, 62.8 (55–70); length of tail, 7.9 (5–10); hind foot, 10.1 (9–11); thunb, 6.3 (5.6–6.7); forearm, 35.7 (34.4–37.4); greatest length of skull, 21.3 (20.9–21.5); zygomatic breadth, 9.3 (8.9–9.8); maxillary tooth row, 7.2 (6.9–7.5); maxillary breadth at M^3, 5.4 (5.1–5.6).

This race occurs in the arid lowlands of western Morelos, and appears to intergrade with *G. s. alticola* in central Morelos, as seen in specimens from Yautepec. Our specimens from western Morelos are typical of the subspecies *leachi*. The upper incisors protrude forward almost parallel to the postero-anterior plane of the skull, and appear crescentic in outline when viewed from above. The color is light brown. The significant differences between *leachi* and *alticola* are not in size (see measurements), but in the morphological character of the incisors and in color. The thunb averages shorter in our specimens of *leachi* from Morelos, with only one individual, a male, reaching 7.0 mm. The thumb measurement of females is shorter than that of males. It should be noted, however, that Hall and Villa (1949) found the thumb to average 7.4 in specimens referred to *leachi* from Michoacan. Apparently the thumb varies in length from population to population.

We found large numbers of these bats in caves, one of which was not much more than a deep pocket in a hillside.

Martinez and Villa (1938) described *Glossophaga morenoi* from Xiutepec, Morelos. These specimens were later lost. The characters ascribed to *morenoi*, except for the absence of a tail, are applicable to specimens of *leachi*. All of our 43 specimens of *Glossophaga* from Morelos have a tail, although it is not apparent on some prepared skins. Because of this, we suspect that Martinez and Villa may have overlooked this structure on their specimens. Using the original description and our own collection as a basis, we feel assured in placing *Glossophaga morenoi* as a synonym of *Glossophaga soricina leachi*.

Glossophaga soricina alticola Davis.—Twenty specimens examined as follows: Jonacatepec, 13; Santa Clara, 7.

Measurements.—Averages and extremes in millimeters of seven males are: total length, 63.1 (57–67); length of tail, 5.6 (5–7); hind foot, 10.3 (6–11); thumb, 7.2 (6.8–7.8); forearm, 36.9 (35.4–38.8); greatest length of skull 21.1 (20.5–21.9); zygomatic breadth, 9.7 (9.4–10.0); maxillary tooth row, 7.1 (6.9–7.3); maxillary breadth at M^3, 5.8 (5.5–6.0). Of six females: total length, 66.2 (63–70); length of tail, 6.7 (6–8); hind foot, 10.8 (10–12); thumb, 7.2 (6.7–7.7); forearm, 36.6 (34.6–37.7); greatest length of skull, 21.0 (20.2–21.8); zygomatic breadth, 9.5 (9.3–9.7); maxillary tooth row, 7.1 (6.8–7.5); maxillary breadth at M^3, 5.7 (5.5–5.8).

This race occurs in the lowlands of eastern Morelos, intergrading with *leachi* in central Morelos. The validity of this subspecies seems assured on the basis of our 13 specimens which agree so closely with the type and paratype from Tlaxcala that the recognition of the eastern race is necessary. The race *alticola* is separated from *leachi* on morphological characters and darker color, rather than on size, although it is slightly larger than *leachi* (see measurements). The upper incisors in *alticola* are much less projected forward and are in a normal position, that is, they are more nearly perpendicular to the postero-anterior plane of the skull (Davis, 1944). They do not exhibit a crescentic outline when viewed from above as in *leachi*. The color is dark sooty in contrast to the light brown of *leachi*. However, a few specimens of *leachi* from Alpuyeca match *alticola* in color.

These specimens of *alticola* were collected near the entrance to a large deep cave. One specimen of *Choeronycteris mexicana* was collected with them.

Our specimens represent the first records of this subspecies in Morelos, and they extend the known range southwestward from the state of Tlaxcala.

Choeronycteris mexicana Tschudi.—Our four specimens (Axochiapan, 3; Jonacatepec, 1) not only represent the first record of this species from Morelos, but also a southern extension of the range, the previous southernmost record being from Tlaxcala (Davis, 1944). The species probably ranges throughout the state, in the semi-desert lowlands.

At Axochiapan these bats were found hanging from the exposed roots of trees growing on the bank of a deep ravine. The foliage hung over the cut excluding sunlight and making a shady retreat. The one specimen collected at Jonacatepec was found hanging near the entrance to a large, deep cave. It flew out of the cave when first disturbed, but immediately returned and was then shot. It shared these quarters with a large number of *Glossophaga s. alticola*.

Leptonycteris nivalis nivalis (Säussure).—One specimen from Huajintlan, in the arid lowlands, seemingly constitutes the first record of this species from Morelos. On geographic grounds our specimen should be within the range of *L. n. yerbabuenae* Martinez and Villa (1940), described from material a short distance from Huajintlan at Yerbabuena, Guerrero. Because the type material was destroyed with the rest of Villa's collection, we follow Hall and Villa (1949) in tentatively assigning our specimen to the subspecies *L. n. nivalis* until topotypes of *yerbabuenae* are available for comparison.

It is interesting to note that in our specimen the lower incisors are absent and there is no indication of alveoli. This has been attributed to accident. The specimen is tailless, the zygomatic arch is complete, there are two premolars and two molars above, and three premolars and two molars below. The wing is noticeably shorter than in representatives of *nivalis* from Texas, due to the shortening of the phalanges of the third finger.

This bat was taken in a cave where it occupied quarters with *Macrotus* and *Chilonycteris*.

Artibeus planirostris planirostris (Spix).—Three specimens were collected at Alpuyeca. The species probably is restricted to the lowlands.

This appears to be a rare bat in Mexico, and this is the first record of its occurrence in Morelos. All of our specimens have the minute third molar. It should also be noted that compared with *Artibeus jamaicensis* from Veracruz the second molar is separated by a conspicuous space from the first molar, whereas in *jamaicensis* the second molar fits closely against the first. Although Hershkovitz (1949) considers *A. planirostris* as a synonym of *A. jamaicensis*, we follow Andersen (1908) until the evidence is more conclusive.

Artibeus hirsutus Andersen.—Seven specimens were taken at Jonacatepec, in the eastern part of the semi-desert lowlands.

Measurements.—Averages and extremes in millimeters of five adult females are: total length, 82.2 (79–86); hind foot, 15.4 (13–18); height of ear, 20.8, (18–21); forearm, 52.9 (48.9–56.3); greatest length of skull, 26.9 (26.6–27.1); zygomatic breadth, 16.7 (16.4–17.2); interorbital constriction, 6.6 (6.5–6.8); breadth of brain case, 11.9 (11.8–12.0); maxillary tooth row, 9.7 (9.6–9.8); breadth at M^2, 11.1 (10.9–11.4). Measurements of one male are: 73, 13, 17, 54.5, 27.6, 16.7, 6.9, 12.2, 9.7, 11.5.

This is the first record of this seemingly rare bat from Morelos. Our specimens extend the known range eastward from the type locality at La Salada, Michoacan.

The minute third molar is present in all but one of our specimens, but this one has the alveolar pits. This species is easily separated from *A. planirostris* by the thickly haired uropatagium, smaller size (see measurements), and by the light grayish color.

A difference in habitat was noted between *hirsutus* and *planirostris* in our field studies. Where *planirostris* was associated with the tropical vegetation along streams, *hirsutus* was found hanging in the dark recesses of an old church in the arid uplands, denoting a preference for caves.

One of our females was carrying a young male half her size. The uropatagium of the juvenile was hairy as in the adults.

Artibeus jamaicensis jamaicensis Leach.—One specimen from Hacienda San Gabriel (Coll. Instituto de Biologia) was examined.

Andersen (1908) reported three specimens from an unknown locality in Morelos. Martinez and Villa (1938) reported specimens from Amacuzac and Las Estacas. We did not encounter it.

Artibeus aztecus Andersen.—Known only from the type locality, this small species of *Artibeus* was described from material taken at Tetela del Volcan, Morelos, on the southern slope of Mt. Popocatepetl. We failed to collect any specimens.

Desmodus rotundus murinus Wagner.—Thirty-one specimens examined, as follows: Alpuyeca, 5; Yautepec, 12; Tlacotepec, 12; Jonacatepec, 2. Found throughout the state in the semi-desert lowlands. Although this bat is wide spread in Mexico, these are the first records from Morelos.

A small cave we visited near Alpuyeca in August was inhabited by a colony of adult females and half-grown young. We failed to find this bat in numerous other caves and grottos searched in western Morelos in 1949, but a large series was collected in caves the following year in the eastern part of the state.

Myotis velifer velifer Allen.—Eight specimens examined, as follows: 2 mi. W Huitzilac, 6; Tres Cumbres, 1; Alpuyeca, 1. Additional records: Las Estacas (Martinez and Villa, 1938); Morelos, no specific locality (Miller and Allen, 1928).

In Morelos, this wide-ranging species is most common in the highlands in association with the pine-fir forest, where it is the commonest bat. It is occasionally encountered in the arid lowlands. This bat emerges at twilight and forages for insects over the small treeless valleys. It retreats to the crevices among the volcanic rocks that are abundant on the hillsides surrounding the valley floors.

Eptesicus fuscus miradorensis (Allen).—We have three specimens from 2 mi. W Huitzilac. In the pine-fir forest association of the highlands of Morelos this bat is nearly as

abundant as *Myotis velifer*. It associates with *velifer* in its evening flight, but tends to feed more about the crowns of the trees.

Martinez and Villa (1938) record eight specimens of *Eptesicus propinquus* from Cuautla. Goodwin (1946:333) gives the following measurements for *propinquus* from Costa Rica: forearm, 40–42 mm.; greatest length of skull, 15.8–16.0. Martinez and Villa record the following measurements for their specimens: forearm, 50.0–53.5; greatest length of skull, 20.0–21.0. These measurements agree with those of *E. fuscus* and also with those of our own specimens from Morelos. For this reason we assign the Martinez and Villa specimens from Cuautla to *E. f. miradorensis*.

Eumops glaucinus (Wagner).–One specimen reported by Sanborn (1932), from an unknown locality in Morelos, is in the U. S. National Museum. We did not find this species.

Tadarida mexicana (Säussure).—Specimens examined, 7 as follows: Huitzilac, 1; Tres Cumbres, 1; Jonacatepec, 4; Santa Clara, 1. The species is probably state wide in distribution.

In the pine-oak forest we captured one specimen that had its daytime retreat under a small boulder on an open hillside. This appears to be an unique roosting place for bats of this species.

Martinez and Villa (1938) record one specimen of *Tadarida brasiliensis* from Cuautla, in the lowlands. If their determination is valid, this would be the only record of this species from Mexico. In two of our specimens from Jonacatepec in the lowlands the breadth at the second molar (7.0 and 6.9 mm.) approaches *T. brasiliensis*. We regard these specimens as *T. mexicana*, but the true relationship between *brasiliensis* and *T. mexicana* is not well understood by us.

Shamel (1931) records twelve specimens of *T. mexicana* from Morelos, but no exact locality is given.

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GENERAL NOTES

SEXUAL MATURITY AND FIRST RECORDED COPULATION OF A 16-MONTH MALE PORCUPINE, *ERETHIZON DORSATUM DORSATUM*

Since there are few detailed records of porcupine copulation in the literature (Shadle, Jour. Wildlife Mgt., 10: 159–163, 1946; Struthers, Jour. Mamm., 9: 300–308, 1928), and no records of exactly how early a male porcupine can successfully copulate and sire young, this paper is offered as a record of the copulation of a captive young male porcupine of known age.

Peterkin, a wild-bred, but laboratory-born and laboratory-reared male porcupine, was born in the University of Buffalo Vivarium on May 20, 1948. The mother was sent to me by Philip Baumgras of the Michigan Department of Conservation. From the time Peterkin was a year old, he has served as a laboratory "testing male" to aid in determining the development and progress of rut in the individual females of our porcupine colony. He began to show considerable sexual urge when he was only five months old, and because he has always been easily handled, he was tried out, and has proved quite satisfactory for the testing process.

At 7:45 P.M. on September 16, 1949, a mature female porcupine, Rosie, showed marked activity and sexual urge, and when placed in the open breeding area with Peterkin, she soon reared on her hind legs and assumed a "male sexual attitude" toward Peterkin. Peterkin's sexual excitement was evidenced by his calling softly in a high falsetto voice, by making the usual male sexual approach with erections of the penis, and by cursory olfactory examinations of the female. All of Peterkin's sex reactions seemed lacking in interest and ardor, in spite of the fact that the female's vaginal area bore a thick odoriferous yellowish discharge. The female called softly to him, repeatedly stood erect on her hind legs, presented her belly and genitals for olfactory examination, and even made several pelvic thrusts like a male, but Peterkin's sex urge showed no particular increase in vigor.

The next morning, September 17, both porcupines in their adjoining cages showed more than usual activity. Facing each other and standing erect on hind legs, with only the cage wire between them, each was doing an exercise dance.

When placed in the open breeding area in the Vivarium, Rosie stood on all four feet with her tail held well above horizontal. As soon as Peterkin was placed with her, Rosie reared and stood erect on her hind feet, walked up to him and made a "typical male sex approach" to him. During this time she frequently reached out with her paws and lightly touched the hairs of Peterkin's lower back and sides, although she made no effort to grasp or hold to

the hairs. This light touching of the hairs generally has a stimulating effect on the sexual urge of the male, which is easily demonstrated under the usual conditions of testing and breeding the porcupines. Peterkin responded in the normal manner and showed more sexual interest and vigor than he had shown the night before.

Peterkin's youth (16 months), small size, light weight, the short length of his copulatory organ, his short hind legs and his complete lack of previous copulatory experience, placed him at considerable disadvantage in copulating with a full grown female. The female did not lift her tail to the normal copulatory position (Shadle, *op. cit.*, 1946), i.e., almost perpendicular to the long axis of the body, but held the tail in an awkward position, where it was in Peterkin's way when he approached from the rear to make sexual contact. He lacked experience in overcoming this disadvantage of the tail extending straight back in a horizontal position, instead of its pointing nearly straight up perpendicularly. The awkward posterior position of the tail altered Peterkin's sexual approach from the normal, direct, posterior position, and forced him to come in from the rear at a lateral angle. In this angular rear approach, the erected penis engaged the more dangerous spine-covered posterolateral region of the female's thigh, instead of contacting the harmless hair-covered genital area. A heavier, mature, experienced, breeding male could have walked straight up in a rear approach and his weight would have lifted her tail or pushed it aside, and the longer legs and longer copulatory organ would easily and readily have made sexual contact.

In the first thirty minutes many unsuccessful efforts to effect copulation were made by the young male, and my attempts to aid him by raising or pushing the tail of the female out of his way disturbed him so much that he was inclined each time to cease his copulatory efforts for a few minutes.

At the end of forty-five minutes of intermittent efforts, sexual contact was established and maintained for approximately a full minute. During this contact the reactions of this young inexperienced male seemed to differ in no apparent way from those of the mature males. His technique, procedure, effort, and vigor were very satisfactory. There appeared to be a definite orgasm, and after the emission the sexual contact was broken. The male immediately squatted on his haunches and, bending his head down, twice performed the cleaning of the penis, apparently with the tongue and lips.

Having completed coition, Peterkin seemed greatly stimulated, for he ran about the cage in an excited manner, and became rather rough in the way he seized, handled, and squalled at the female. Ordinarily he is quite gentle with the females, unless one attacks him while he is sexually aroused, and then he may retaliate.

During the next 30 minutes Peterkin's sexual urge decreased and although several more copulatory attempts were made, he did not succeed again in solving the problem of the awkward position of the female's tail. During all this time Rosie continued to register marked sexual desire and receptivity, but Peterkin was fatigued and he finally stretched out and went to sleep, and was returned to his own cage. Nine hours later, neither porcupine was at all interested in the other.

This is the first record of a male porcupine of this age having copulated, and having sired offspring. Peterkin was born May 20, '48, served his first female September 17, '49 at the age of approximately 16 months, and 210 days after copulation, a 542 gram porcupette (nursing young) was born in the Vivarium (Shadle, Jour. Mamm., 29: 162–164, 1948; *Ibid.*, 32: 219–221, 1951).

Struthers (*op. cit.*, 1928) says that the porcupine reaches "maturity" at the end of the third summer (when approximately 28 months of age), at which time "it wanders far from the home den," and he also states that by "the third autumn the female has reached the age of maturity." Although not expressly stated, Struthers apparently means sexual "maturity," for in the following paragraph he says, "After the third year the animals still continue to grow until they reach an average weight of fifteen pounds."

This statement of the time of sexual maturity is about a year later than the case of Peterkin cited above. It seems unlikely that Peterkin's development is just a single isolated case, for a second parallel case is developing in the laboratory now. Danny, a wild-born

porcupine, and his mother were captured and brought into the Vivarium. At the age of five months he showed considerable sexual drive and at the age of one year showed excellent promise as a "testing" and "breeding" male for the Vivarium porcupine colony. The development of Danny's sexual drive has paralleled or possibly slightly exceeded the pace set by Peterkin in his sex development of his first year. Danny, at one year of age, was as large as Peterkin was at two years of age, but in testing the females, Peterkin's greater experience gave him a decided advantage over Danny. Peterkin is now vigorous, delivers a copious urine shower, is insistent in his sex advances on the female, and has developed much more self-confidence in dealing with a recalcitrant female when she squalls at him, or attacks him. Peterkin readily holds his own and may even subdue the female and then continue his courting or copulatory efforts with her.

While Danny at one year of age shows considerable sex drive, vim, and vigor, he has a rather youthful indecisive manner of sex approach, and a squalling, antagonistic female may quickly discourage his sex urge, drive him away, or turn his attentions to other females.

The two cases just cited together with many other observations of young male porcupines definitely suggest that *sexual maturity in the male porcupines* may be attained much earlier than has been supposed. We have definitely established that the male porcupine may become a sire as early as approximately 16 months of age.

This investigation was supported in part by grants from the Committee for Research in Problems of Sex, National Research Council.—ALBERT R. SHADLE, *The Vivarium, Biology Dept., University of Buffalo, Buffalo 14, New York.* *Received July 15, 1951.*

NEST AND BEHAVIOR OF A SHORT-TAILED SHREW, *CRYPTOTIS PARVA*

On February 10, 1950, one of my biology classes from Stephen F. Austin State College found three young *Cryptotis parva* and their parents in a pasture by Bonita Creek on the northwest edge of Nacogdoches, Nacogdoches County, Texas. The shrews' nest lay on the surface of the ground underneath a large piece of corrugated sheet metal, and was about one hundred feet from a marsh containing cattails and dense grasses.

When the piece of metal was lifted, the mother shrew ran about rather aimlessly a few feet from the nest and was easily caught. About three feet away we later found an adult male. He had been accidentally squashed under the metal roof.

The nest was a loose pile of old willow leaves, seven inches in diameter and about two inches high, lying in a shallow depression on the ground. The three young shrews were on top of the leaves in a small hollow, but soon after their roof was lifted off, they began to squirm out of sight. They burrowed into the leaves and one managed to hide in a tunnel under the nest. We put them back on top of the nest for photographs and then examined their home and its surroundings.

Two runways connected with the nest, one by means of a short tunnel leading from the bottom and the other from the side. There was a toilet area about three inches in diameter at the edge of the nest where a considerable number of small beetles, larvae, and small flies had gathered.

At the college the female shrew was put into a washtub partly filled with sand and leaves, and soon she fed on a white-crowned sparrow carcass. The three young ones were photographed and examined and then placed in the cage with their mother two hours later. She bit one of them to death as soon as she discovered it, and about fifteen minutes later she pulled another one under some leaves and ate one-fourth of its body. Overnight the third young shrew was entirely eaten except for one of its legs. Apparently the strange new surroundings and the excitement caused the mother to destroy her family in this way.

For two months and a half I kept the shrew in the tub and watched her behavior. Her general actions were like those of other shrews I have seen. Almost all movements were rapid as she scurried about, and often she held her nose in the air, sniffing and quivering the vibrissae. She rested and slept frequently in a favorite spot under an oak leaf. Smooth circular tunnels about 15 millimeters in diameter were dug in the sand, and several burrows ran under the metal pan of water lying on the floor of her cage. She voluntarily swam across the

pan at various times with surprising ease. Her body floated so high on the water that she seemed to run on the surface. Among the things she ate in captivity were mouse carcasses, birds, a lizard, crickets, and apples.

The shrew died on April 28 (due to my neglect), and her weight at that time was 3.6 grams as compared with 4.6 on February 10 when she was captured and 4.5 on February 18.

The young shrews weighed 2.1, 2.2, and 2.1 grams, respectively; the adult female weighed 4.6 grams, and the male weighed 5.6 grams. The young (Pl. I) had long pointed heads that measured 15 millimeters in total length, 7 in width, and were 5 millimeters deep through the eye region. The distance from eye to end of nose and from eye to ear was 5 millimeters. In one of the young the genital opening was one millimeter from the anus.

The long nose was pink and swollen at the tip, and the belly, front legs, and hind feet were also pink. The skin was loose and wrinkled, and a dense growth of hair (less than one millimeter long) covered the top of the head, neck, back, and sides. Only a very few short, scattered hairs were on the belly and the ventral surface of the neck. The tail was hairless,

PLATE I

Young *Cryptotis parva* about one week old. There is a dense covering of very short fur on the dorsal areas, and eyes and ears are closed

plump, and pink, and constricted at the base. There were many short white hairs on the chin. The toes were largely united and the toenails unpigmented.

The young shrews could not walk or raise their bodies from the ground, although they could crawl and squirm about rather well with the help of their front legs. The light and heat of a photoflood lamp made them particularly active just when I wanted them to pose for their portraits. As far as I could detect, they uttered no sounds.

The age of the three shrews may be estimated fairly accurately from the data on development of a family of five *Cryptotis parva* studied by Hamilton (Jour. Mamm., 25: 1–7, 1944). His animals averaged 1.3 grams at birth and increased by a tenth to a fifth of a gram daily for about three weeks. Assuming that my shrews grew at the same rate, they were one week old when discovered.

In their remarks on the life history of this shrew in Texas, Davis and Joeris (Jour. Mamm., 26: 136–138, 1945) pointed out that there were no breeding records for the months of November to February. Recently Hunt (Jour. Mamm., 32: 115–116, 1951) reported the discovery of a male, female, and four young in a nest from Brazos County, Texas, on February 25, 1950. Surprisingly enough, he found the nest under a piece of tin just as we did. He estimated that the young shrews were two weeks old, which means that they were born on February 11. Our shrew family presumably was born on February 3 and was conceived during mid-January. Neither the gestation period nor the number of litters per year are

known for this species. Since our shrew did not have a second litter during her two and a half months of captivity, it seems unlikely that effective mating took place during the week following the birth of her young. I do not know what effect the weather might have had in regard to this early breeding of *Cryptotis parva*, but the winter of 1949–50 was a relatively mild one during which no snow fell at Nacogdoches.

Another of these shrews was caught by Hollis Alford in grass at Blount's Lake, nine miles southwest of Nacogdoches. We took a number of *Reithrodontomys* in the same trap line, and a few hundred feet away at the edge of the lake caught *Sigmodon hispidus* in cattails and *Peromyscus nuttalli* in scrubby oak-pine woods. I suspect that these shrews are more abundant in this area than is apparent from the catch, as I have seen a few fields with networks of tiny burrows that would only accommodate an animal of this small size.

Perhaps the family life of these animals is a cooperative affair. At any rate it seems significant that both Hunt (*op. cit.*) and I caught a nursing female and an adult male at the nest. My male appeared to be in breeding condition as the sexual organs were large. The testes measured 2.5 by 3.5 millimeters. The everted penis had a basal section 6 millimeters long and a distal part (glans) 5 by 3 millimeters.

Further evidence of gregariousness has been noted by Hamilton (Jour. Mamm., 15: 154–155, 1934), who found nests with three adults in one and five in another. Davis and Joeris (*op. cit.*) found the amazing number of 12 adults in a single nest on December 6 near College Station, Texas.

Careful studies of the natural behavior of these tiny shrews are needed to explain these observations and to fit them into the year-round activities of this interesting animal.—Harold E. Broadbooks, *Dept. of Zoology, Univ. of Arizona, Tucson, Arizona.* *Received June 22, 1951.*

ANTING NOT EXCLUSIVELY AN AVIAN TRAIT

On June 27, 1951, in my yard in Holyoke, Massachusetts, I observed anting being performed by a Gray Squirrel, *Sciurus carolinensis*. My attention was drawn to the animal by the unusual actions it was repeatedly performing on the same patch of bare ground beneath a Colorado Blue Spruce, *Picea menziesii*. These actions were varied. Occasionally the squirrel crawled on its belly across the spot. Again, it rolled its shoulder and back onto the spot, deliberately, in the manner of a dog rolling in filth. A third gesture involved a forward somersault, after which the squirrel rolled on its side like a kitten playing with a ball. This varied performance, which brought virtually all surfaces of the squirrel in contact with the ground, continued for about five minutes; the one particular patch of ground was used in all cases. The actions of the animal appeared deliberate and intentional. Eventually the squirrel walked slowly away. When I examined the spot immediately afterward, I found that the squirrel had been rolling and rubbing itself on part of a "trail" along which small brownish ants were passing in some numbers. Further, the patch of ground on which the squirrel performed the above-described actions was occupied by at least three ant holes, from which the insects were issuing. I saw the squirrel scratching itself two or three times during the above performance.

The only other case of anting I have observed occurred less than fifty feet away. About April 1, 1949, I saw two Slate-colored Juncos, *Junco hyemalis*, anting in my yard in the manner which is abundantly described in the ornithological literature. In both cases, the weather was relatively warm and humid.—Aaron M. Bagg, *Holyoke, Mass.* *Received July 9, 1951.*

DOG LOCATES WINTER NESTS OF MAMMALS

Mammalogists are aware that trapping alone does not provide much information about the living quarters of small mammals. Recently, it was the authors' good fortune to attend several 'mouse hunts' with friends at Old Lyme, Connecticut. Mr. Walter Peters, the caretaker of Dr. Warren McCulloch's farm at Old Lyme has a small Labrador Retriever, 'Rusty,' with an unusual ability to find the nests of small mammals. During January and February,

accompanied by various people, Rusty ferreted out countless nests of *Peromyscus leucopus noveboracensis* (Fischer), as well as the nest of four *Clethrionomys* and the nest of two *Glaucomys*. All the nests were found in a second-growth forest, typical of the region, composed largely of oaks, hickories, and a scattering of old-field red cedars. Brief descriptions of some of the nests found follow:

On March 3, 1951, one nest was found under a large flat rock, roughly three feet square. The nest was relatively new, made of grass and a few leaves. It contained five yearling mice (*Peromyscus*), only three captured, all females. One nest was twenty-one feet up in a hemlock, in the floor of a grey squirrel nest that was in use; it contained two yearling *Peromyscus*, a male and female. The nest was composed of grass and shredded cedar bark, apparently from material collected by the squirrel. On March 10, 1951, a *Peromyscus* nest was found in a rotten stub of a hickory, about six feet high. The nest hole was about five feet up, and apparently formerly occupied by a chickadee, judging from the nest material. One very reddish, obviously old, female and two yearlings, male and female were in the nest. One nest, containing three yearling *Peromyscus*, two females and one male, was found in a hollowed-out stub of a branch on a large windfall elm. The nest was constructed of leaves and grass, and apparently used a long time, judging from the accumulation of semi-decayed nest material.

In February, 1951, we located a nest in a large oak log. It was constructed of shredded cedar bark and moss and contained six yearling *Peromyscus*, all females. Another nest, with four *Peromyscus*, was found underneath a woodpile. Three *Peromyscus* were found in a stub about five feet high with the nest in a hollowed-out portion about three feet from the ground.

The nest of four *Clethrionomys* was found in a hollowed-out nest hole in a small (six inches in diameter) fallen hardwood. The nest of *Glaucomys* was found at the base of a large, dead almost completely hollowed-out cedar. The nest was barely six inches above ground level.

All of the *Peromyscus* nests contained large numbers of fleas, the vast majority of which were *Orchopeas leucopus* (Baker). Ninety specimens of this flea were found in one nest alone. All of the nests contained small numbers of *Epitedia wenmanni* (Rothschild) and *Stenoponia americana* (Baker).

While following Rusty, we quickly found it was useless to call his attention to various places that we considered potential nest holes. We could never interest him in any of them. He found all of the nests on his own, and would even attempt, sometimes successfully, to climb trees to get at them. Using the dog, we learned more about the winter nests of mice in a very short period than we had ever learned before. We could expect to find three or four nests in a single afternoon's walk. This experience has convinced us that such a dog is a useful adjunct to the mammalogist's standard equipment.—ROBERT L. EDWARDS AND WALTER H. PITTS, *Biological Laboratories, Brandeis University, Waltham, Mass., and Department of Mathematics, Massachusetts Institute of Technology, Cambridge, Mass.* *Received May 21, 1951.*

THE GRAY FOX ATTRACTED BY A CROW CALL

In connection with recent studies of the bird population of the Shenandoah National Park it became of interest to check on the breeding crow population through specimens. On June 5, 1948, with W. M. Perrygo, I was on a branch of North Thornton River near the bridge on Route 211, above the town of Sperryville, Virginia. While I rested on a stone wall under the cover of a spreading tree, using an Olt crow call, with a mixture of adult and young caws and squawks appropriate to the season, Mr. Perrygo crouched in an indistinct trail under shelter of bushes, 75 feet below me.

I had hardly started calling when, with a rush, a gray fox (*Urocyon*) came up the trail so intent on the sounds I was producing that my companion was not identified as a man, but only as an obstruction in the way. I had a glimpse of gray fur as the fox jumped onto my friend's head and shoulders and then, as Perrygo sprang to his feet even more startled than I was, saw the fox lying on its back with its feet in the air for a brief instant in a mat of honeysuckle before it streaked away.

I have been reminded of this highly amusing incident by a letter which Joseph W. Lippincott wrote to the editor of Pennsylvania Game News, published in the number for April 1951, page 62, as follows:

"While calling crows to the gun I have at the same time lured gray foxes to within a few yards of me on three different occasions. Two of these I shot; the third I spared because it was in the territory of a fox hunting club. How many other foxes have come to my crow call and not been noticed among the bushes I can only conjecture, but I believe the squawk which completely fools the crow likewise completely fools the fox, just as it does the Cooper's hawk. All three foxes acted alike. They came through cover as if stalking me; then made a rush for my hiding place.

"The fox that I allowed to escape charged into the crow decoys that I had set up on bare ground and was seizing one of them when I surprised him with such a yell that he dashed away. Maybe it isn't easy to call crows with one eye focused in the air and one on the ground, but if you know crowtalk and want an occasional fox, it's worthwhile."

From these two separate observations in Virginia and Pennsylvania it would seem that the crow may figure as a fairly usual item of food with the gray fox.—ALEXANDER WETMORE, *Smithsonian Institution, Washington 25, D. C.* *Received June 23, 1951.*

DIVING DEPTHS OF THE STELLER SEA LION AND ALASKA FUR SEAL

Naturalists seldom have the chance to observe the Steller sea lion (*Eumetopias jubata*) and the Alaska fur seal (*Callorhinus ursinus*) off shore where information on their diving habits is available. Fishermen using set lines and nets on off-shore fishing grounds are often afforded an ideal opportunity to gather such information. Unfortunately fishermen seldom make their observations known. On a recent stay in Sitka, Alaska, I visited at length with Mr. Herman Kitka, a Tlingit fisherman and sealer who has become familiar with the waters and sea mammals off Sitka during a period of more than thirty years. I spent nearly two weeks with Kitka at his sealing camp in the latter part of March 1950. During our many conversations and trips afield I found him an intelligent and accurate observer of wildlife.

With the aid of a nautical chart Kitka pointed out where he had been bothered by sea lions during fishing operations. These areas are the halibut fishing grounds off the mouth of Sitka Sound, off Crawfish Inlet, and off Kruzof Island, all within about 40 miles of Sitka. On these fishing grounds he frequently brings up fish from which sea lions have taken chunks, and sometimes even the sea lions themselves. The depth of water in which he fishes ranges from 30 to 130 fathoms. The sea lions he brings up on his lines are small ones, weighing less than 200 pounds. Larger animals, when hooked, are able to break the lines and escape. Missing hooks and broken lines indicate that this sometimes happens. He has never found evidence that sea lions descend below 100 fathoms. Even at this depth signs of sea lions reaching the bottom are very scarce. Most fish damaged by sea lions, as well as drowned animals, are recovered from depths up to 60–80 fathoms.

Kitka is quite certain that the sea lions are hooked on the bottom. Animals are recovered when none were in the area at the time the line was set, thus they were not hooked while taking bait as the line went out. When hooked animals are brought aboard they are dead and show evidence of having been dead for sometime. Additional evidence that the sea lions reach the bottom is afforded when the animals are seen at the surface eating halibut before recovery of the line has begun. As the line comes aboard Kitka finds halibut heads on the hooks from which the body has been torn. When a sea lion locates a hooked fish it tears at it with powerful jaws. If the fish is a small one the hook often holds the head and the animal surfaces with the remainder of the fish. Here, with a firm grip on part of the fish, the sea lion shakes its head violently from side to side, tearing away a large chunk which it swallows before retrieving the remainder. The process is repeated until the entire fish is devoured or the sea lion's appetite is satisfied. The marks left on fish by a sea lion's sharp ripping teeth are quite characteristic, Kitka says, leaving little doubt, when a line is recovered, that a sea lion has visited it. It is not uncommon for sea lions to damage fish when

lines are in water deeper than 100 fathoms. The strategy of the animals when this is the case is to wait for the fisherman to begin to pull in his line. While the catch is on its way to the surface the sea lion dives to a safe depth, tears a fish from the line, then surfaces to consume the stolen meal at a distance safe from gunfire.

"Sea lions are too smart to get caught on the same hook as the fish. They are never hooked in the mouth. They get hooked near the tip of one of the front flippers," Kitka says. The way in which this might happen seems quite logical. At the surface the sea lion sees a set line marker and dives to investigate. Swimming in the dim light near the sea floor one eye must be near the line in order to follow it. Thus the lower flipper must sweep close to the bottom, even brushing it at times. Should the animal pass an empty hook at such a moment the hook may be picked up in the tough skin and cartilage of the flipper and unless the animal is large enough to break the line it soon drowns.

Although Kitka's experience leads him to believe that the Steller sea lion is capable of descending 100 fathoms (600 feet) below the surface and often reaches a depth of 60 to 80 fathoms (360 to 480 feet) he says the same is apparently not true of the fur seal.

Kitka states that fur seals are often about when he is fishing, yet he finds no evidence that they descend much deeper than 30 fathoms. "They will sometimes get hooked on a line when it is going out or coming in where the water is deep but they can't go down as far as sea lions. The fur seal takes little round bites that are a lot different from the big ones taken by sea lions. In shallow water, about 30 fathoms, a fur seal will swim along a line and rip strips of skin from hooked fish, looking for choice ones," Kitka says.

Kitka's observations on the depth of diving of the fur seal are in line with data published by Scheffer (Murrelet, 27:25, 1946), reporting several fur seals taken in fishermen's nets at depths of from 4 to 40 fathoms (24 to 240 feet) off the coast of Oregon.—KARL W. KENYON, *U. S. Fish and Wildlife Service, Seattle, Washington.* *Received April 30, 1951.*

LITTER SIZE IN THE BLACK BEAR

Two and three cubs in a black bear (*Ursus americanus*) family seem to be equally common. Litters of four are not extremely rare, a recent case being that of quadruplets taken from a den in early May, 1950, and exhibited by Armand Pomerleau of Jackman, Maine. Other recent occurrences of quadruplets have been noted in Pennsylvania and elsewhere. Reports of quintuplets and at least one mention of sextuplets have been found in newspaper files.

In March, 1951, while on a collecting trip in Alpena and Presque Isle counties, Michigan, occurrences of two litters of five cubs each were noted and substantial testimony secured.

On March 20, 1951, the writer accompanied District Supervisor C. A. Eagle of Gaylord, Michigan, to call on a Mrs. Burr who captured three of a litter of five cubs. Unfortunately neither Mrs. Burr nor her son were at home. Mr. Harrison, a near relative, confirmed the incident. Mr. Eagle's letter of March 26, 1951, follows:

"Relative the fact that in 1923 I had positive evidence of one female (black) bear having five cubs. As I told you, I was manage of the Beaver Lake Hunting and Fishing Club from 1921 to 1927, and at that time it was leg. have bear cubs under permit as pets.

"I ran an advertisement in the Alp aper to buy cubs for the Club. One day I received a call from a Mrs. Burr that she had three cubs. I contacted her and bought the cubs for $75. She gave me the following story of how she caught the cubs:

"Mrs. Burr and her small son, then about eight or nine years old, were going to their farm by team and wagon. Their home was on M-32 about nine miles west of Alpena. When they were about a quarter of a mile from their home they came upon an old bear and five cubs. Three of the cubs ran up a small tree and two of the cubs ran away with the mother bear. Mrs. Burr kept the three cubs up the tree while her son walked to the farm and got some bags to put them in. Mr. Harrison, who is Mrs. Burr's brother-in-law, confirmed this on March 20, 1951, when we talked with him at his store ten miles west of Alpena.

"I am of the opinion that you obtained the story from Officer Ned Curtis, regarding the five cubs killed last year (1951) in Presque Isle County near Hawks, Michigan."

In May 1950 two farmers of Presque Isle County, Michigan, killed a mother black bear and her five cubs. On complaint filed by Conservation Officer Ned Curtis, the two men were arraigned before Justice A. L. Sabin of Rogers City, Michigan. They were found guilty and fined for killing the five cubs. Commenting on the incident Officer Curtis said, "We appreciate the fact that Mr. Claus was within his rights in disposing of the adult bear. We cannot, by any stretch of imagination, see where Mr. Claus and Mr. Krueger were justified in killing (her) five helpless little cubs. Otto Failing, District Game Manager at Gaylord, told me that there had been only one other authentic report of a black bear in Michigan having five cubs."

There is reason to believe that the average number of cubs of the black bear is higher than commonly credited. Cubs are seldom discovered before they are about two months old, by which time infant mortality due to natural hazards may have taken a toll.

A female can nourish only a certain number of cubs, that number being determined by the amount of her fat reserve and the date of her release (by weather) from confinement to the nursery which, in the north, may not be until mid-April or May. During this period of confinement, which has been known to extend to twelve weeks, the female provides nourishment solely from her reserve.

Even under the favorable conditions of an adequate reserve and an early spring, the female must nourish the young largely from her reserve over the lean months of spring and early summer until ripening fruits afford an ample diet. Under the unfavorable conditions of an inadequate reserve and a late spring, her capacity to provide nourishment would be limited and the survival of cubs affected accordingly.

In several instances a tendency to abort, when flushed from the winter nest, has been reported of females nearing parturition. In a recent case, a Pennsylvania Game Protector secured a cub thus ejected and kept it alive at his home for about two weeks. Premature cubs seldom survive under human care.—J. R. Matson, *Perry, New York. Received May 12, 1951.*

TRIPLET ALASKAN MOOSE CALVES

On September 7, 1950, the writers were camped on an unnamed lake northeast of Lake Minchumina in south-central Alaska. In the evening a cow moose was observed feeding with her calves in an open, swampy area bordering the lake. She was approached to a distance of about 200 feet and then called up to about 100 feet from the willows where the observers were located. After apparently making out the cause of the disturbance, the cow started across shallow water toward the shore and for the first time was observed to be followed by three calves. These were very evenly matched as to size, but small considering the time of year. They followed the mother directly to cover on the shore. The animals were at least an eighth of a mile from cover which could have concealed another cow and there seemed to be no question that the calves were triplets. This is such an unusual occurrence that it seemed worthy of recording.—N. W. Hosley and Frank S. Glaser, *Fish and Wildlife Service, College and Fairbanks, Alaska. Received April 23, 1951.*

EVIDENCE OF A LATE BIRTH FOR THE RACCOON

A lactating female raccoon (*Procyon lotor lotor*) was captured on November 25, 1950, in the yard of Mr. Theodore Moore of Valley Head, West Virginia. The animal was in an emaciated condition, and had ventured out in a snow storm when drifts were already from two to two and one-half feet deep. The raccoon was forced by the snow drifts to follow a course along a small brook which ran through Mr. Moore's yard, consequently it was set upon by Mr. Moore's dogs. Mr. Moore rescued the animal and took it into his home, where it lived for a week and once accepted some lean meat, on November 27, before it died. The carcass remained frozen throughout the winter in a suspended bucket in some nearby woods.

Two West Virginia Game Technicians, Sturgis McKeever and Edward Berard, recovered the body in February, photographed it, and removed the skull and mammary tissues after making standard body measurements.

Blunt, rounded canines, 12.0 mm. in length and 22 mm. from tip to tip, possessing cracked enamel, along with well-worn molars and the ankylosed skull, indicated that the raccoon was an adult of at least two and probably three years.

Four small cubs were shot during the final week of December by Mr. Moore and a neighbor in the same area near Mr. Moore's residence. One of the pelts was recovered, but the other three were sold. The remaining pelt measured 620 mm. in total length with a tail measurement of 197 mm. These cannot be considered as true measurements, but are offered to serve merely as an indication of size. By way of comparison, a cub raccoon taken in West Virginia on July 27, 1950, measured 612 mm., including a 204-mm. tail, while three adult raccoons from West Virginia had an average total length of 759 mm. with an average tail measurement of 245 mm. These were body measurements, not skin measurements.

Allowing a normal period of three months for lactation for *Procyon lotor*, it can be calculated that the animal gave birth to young no sooner than August 15, 1950, whereas normal births are usually before May 15 each year. The size of the cub, if it were hers, seems to substantiate this theory.—Edward V. Berard, *Division of Game Management, Conservation Commission, Elkins, West Virginia.* *Received April 28, 1951.*

ENDOPARASITES OF MUSKRATS IN THE VICINITY OF HAMILTON, ONTARIO

In recent years a number of investigations carried out in Europe and North America have indicated the muskrat, *Ondatra z. zibethica* Linn., to be the host of a variety of species of parasitic helminths.

A marked decline in muskrat numbers occurred during 1947 in the vicinity of Hamilton, Ontario. This population decrease was most obvious in the Dundas Marsh and the environs of the Hamilton Bay. An investigation was made in 1948 and 1949 to determine the species of helminths and their incidence in the muskrats collected from the region.

In March, 1948, 53 muskrat carcasses were procured from trappers in the Hamilton Bay district, and in March, 1949, 55 carcasses were collected from the Dundas Marsh. All were stored in a freezing compartment where they remained in excellent condition until they could be examined during the summer months. At the time of autopsy the carcass was examined superficially for obvious pathological conditions. The surface of the carcass was examined for any evidences of filariid worms, but complete diagnosis was impossible because the pelt of each muskrat and many of the hind legs had been removed previously by the trapper. The alimentary tract was sectioned and, like its contents, washed and examined. The reproductive organs, urinary bladder, kidneys, liver, gall bladder, lungs, and heart were all examined. The different types of parasites were observed in 1948, and the incidence of the different species was ascertained in 1949 (Table 1).

The percentage of trematodes found was much higher than that of cestodes and nematodes. *Notocotylus quinqueserialis* infected the greatest number of muskrats and produced the highest concentration in any one animal. The caecum of one muskrat harboured 989 of these flukes, but the animal appeared totally unaffected, a fact which lends support to Mönnig's statement (1947:66) that the members of the family Notocotylidae are "... usually considered to be relatively harmless."

The monostome, *Catatropis filamentis*, parasitized 27 of the muskrats examined from the Hamilton Bay. In all instances its site was the small intestine. In the five animals infected with this trematode from the Dundas Marsh, however, all the flukes were removed from the large intestine.

An examination of the internal organs revealed a large ball of matter, two centimeters in diameter, from the urinary bladder of an adult female which showed no cell detail or architecture, and was diagnosed by the Pathology Department of the Ontario Veterinary College as "coagulated exudate."

This investigation reveals that at Hamilton the muskrats are more heavily parasitized with a greater variety of helminths than are the muskrats of Ohio (Rausch, 1946) and New York (Edwards, 1949). More species were reported by Law and Kennedy (1932) at Kirkfield, Ontario (100 miles northeast of Hamilton), but the incidence was not stated.

The finding of *Metorchis conjunctus* in the muskrat is unique as no previous record of its occurrence in this animal has been found, and Cameron (1944) states that it has not been found naturally or experimentally in rodents. The metacercariae in the Lake Edward area, Quebec (Cameron, 1944), were found only in the common sucker (*Catostomus commersoni*). This fish is known to occur in the vicinity of Hamilton, but the stomach of the infected muskrat contained only plant matter at autopsy. This was the commonest component of the food of the 108 animals examined, and indicates (during March at least) that muskrats nclude few fish and other animals in their regular diet.

An adult *Alaria mustelae* was found in one muskrat in this investigation, and Law and Kennedy (1932) reported it from muskrats at Kirkfield. Adults were found naturally in mink and weasel by Bosma (1931), and she found the metacercariae of this fluke in the muscles and lungs of mice, mink, and raccoon. This, like *M. conjunctus*, indicates that muskrats do occasionally include animals in their diet.

TABLE 1.—*Endoparasites of the muskrat in the vicinity of Hamilton, Ontario*

PARASITE	LOCATION IN HOST	DUNDAS MARSH 1949 (55 CARCASSES)				HAMILTON BAY 1948 (53 CARCASSES)	
		Hosts Infected	Number of Parasites		Per Cent Infected	Hosts Infected	Per Cent Infected
			Average	Extremes			
Trematodes							
Notocotylus quinqueserialis (Barker & Laughlin)	caecum	50	82.6	1–989	90.9	38	71.7
Echinostomum coalitum (Barker & Beaver)	small intestine	48	13.6	1–113	87.3	25	47.2
Catatropis filamentis (Barker)	large intestine	5	16.4	1–60	9.1	—	—
Catatropis filamentis (Barker)	small intestine	—	—	—	—	27	50.9
Plagiorchis proximus (Barker)	small intestine	4	43.0	1–114	7.3	8	15.0
Echinoparyphium contiguum (Barker & Bastron)	small intestine	—	—	—	—	2	3.7
Echinostomum callawagensis (Barker & Noll)	small intestine	—	—	—	—	1	1.9
Alaria mustelae (Bosma)	small intestine	—	—	—	—	1	1.9
Metorchis conjunctus (Cobbold)	small intestine	—	—	—	—	1	1.9
Cestodes							
Hymenolepis evaginata (Barker & Andrews)	intestine	26	—	—	47.3	16	30.2
Cysticercus fasciolaris (= *Taenia taeniaeformis* (Batsch))	liver	1	—	—	1.8	—	—
Nematode							
Trichuris opaca (Barker & Noyes)	caecum	1	—	—	1.8	—	—

All the remaining flukes are recorded from muskrats at Kirkfield, but Rausch in Ohio reported only three of these (*E. coalitum*, *N. quinqueserialis*, and *P. proximus*), and only two of them (*N. quinqueserialis* and *P. proximus*) were found by Edwards in New York. They are bracketed in their order of abundance and frequency as related to one another. Although Edwards did not find *E. coalitum*, he did report *E. revolutum*.

The two tapeworms and one species of roundworm found in this investigation were also reported from Ohio (Rausch did not state the species of *Hymenolepis*) and New York. Although the tapeworms were found at Kirkfield, the roundworm was not.

The effect of the parasites on the health of the muskrats appeared minimal, even though heavy infections were often encountered. It is doubtful that the helminths recorded in this survey could account for the drop observed in the muskrat population in 1947. Dr. L. P. E. Choquette (personal communication) believed that muskrats could harbour a large number of *Hymenolepis evaginata* without detrimental effects, but a severe infection of the liver with the larval cestode, *Cysticercus fasciolaris*, could be detrimental. Since there was only a single infection of this cestode in the carcasses collected in 1948 and 1949, it appears unlikely that *C. fasciolaris* was at an injurious level during 1947.

This research project was made possible by a grant from the Ontario Research Council. The writer is indebted to the late Dr. A. E. Warren of McMaster University for his guidance and interest in this work, and to the university for the facilities that were provided. Particular thanks are extended to Dr. L. P. E. Choquette of Macdonald College of McGill University who identified representative specimens of each parasite. An expression of appreciation is extended to Dr. D. M. Davies of the Ontario Research Foundation who read and criticized this paper.

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G. K. Sweatman, *Dept. of Zoology, Hamilton College, McMaster University, Hamilton, Ontario.* *Received May 5, 1951.*

LONG-TAILED SHREW (*SOREX DISPAR*) IN MARYLAND

Since the publication of records of the long-tailed shrew, *Sorex dispar* Batchelder, in Pennsylvania (Rhoads, Mammals of Pennsylvania and New Jersey, 1903; Poole, Reading Public Museum and Art Gallery, Bull. (1):11, 1932) and West Virginia (Howell, Proc. Biol. Soc. Wash., 24:98–99, 1911), as well as its hypothetical occurrence in Virginia (Handley and Patten, Wild Mammals of Virginia, 1947), it has been sought for in Maryland. Gardner (Proc. Biol. Soc. Wash., 63:65–68, 1950) indicates that the species should occur in Maryland, but he cites no records.

Three specimens were collected on September 6, 1950, at Muddy Creek Falls, in Swallow Falls State Forest, Garrett County, at an altitude of approximately 2200 feet. The shrews were captured in snap traps placed on ledges in crevices of outcropping sandstone two or three feet above a small stream's level. The traps were baited with a combination of peanut butter, bacon, oatmeal, and raisins. All three were adults as evidenced by a bare and rounded tail tip.

The habitat generally agrees with the information supplied by Richmond and Grimm (Ecol., 32(2): 279, 1950) for *Sorex dispar* in Pennsylvania. The Muddy Creek Falls locality is a relatively cool, moist, hemlock and rhododendron forest, directly adjacent to a clear mountain stream that culminates into the steep spectacular falls. *Sorex dispar* was captured in the same microhabitat with the red-backed vole (*Clethrionomys gapperi*), short-tailed shrew (*Blarina brevicauda*), deer mice (*Peromyscus maniculatus* and *P. l. noveboracensis*), and jumping mouse (*Napaeozapus insignis*).

Sincerest appreciation is extended to Dr. J. Kenneth Doutt, curator of mammals, Carnegie Museum, Pittsburgh, for verifying the identification of the specimens.—Romeo Mansueti and Vagn F. Flyger, *Maryland Department of Research and Education, Solomons, Maryland.* *Received June 26, 1951.*

THE DWARF SHREW, *SOREX NANUS*, IN NEW MEXICO

On August 2, 1939, a dwarf shrew was captured by William J. Koster beneath a log a few yards from Gallinas Creek in the Sangre de Cristo Mountains, in Section 13, Township 17 N, Range 14 E, San Miguel County, New Mexico. This is approximately 13 miles northwest

of Las Vegas. The animal was kept alive in a jar for a few hours during which time it was fed grasshoppers.

A survey of the literature indicates that this is the first record from New Mexico and that records from other areas are scarce. Apparently six specimens have been reported from four localities in Colorado and one each from Arizona, Wyoming, and Montana. The specimen from the last state appears to be lost.

The New Mexico specimen, a male with unworn teeth, is preserved as a study skin and skull (No. 121) in the mammal collection of the University of New Mexico. The following measurements were taken in millimeters: total length, 86; tail vertebrae, 38; hind foot, 11; condylobasal length, 14.8; palatal length, 6.1; cranial breadth, 7.2; interorbital breadth, 2.9; maxillary breadth, 4.2; maxillary tooth row, 5.4.

The region of capture is immediately above the limit of agriculture at the eastern edge of the Santa Fe National Forest. The valley at this point is narrow with steep, heavily wooded sides. The nearly level valley floor seems to consist of old beaver meadows, now largely covered with a growth of alder, willows, and a few aspens. The warmer slope of the canyon is covered with ponderosa pine while the cooler slope, adjacent to which the shrew was taken, is closely covered with a mixture of white and Douglas firs. An anaeroid barometer indicated an elevation between 7500 and 7600 feet.

The area was revisited on May 5 and 6, 1951, with a mammalogy class in the hope of securing additional specimens. Over 400 traps, mostly of the mouse and museum special types, were set but no *Sorex nanus* were taken. The catch consisted of *Thomomys bottae fulvus*, *Peromyscus maniculatus rufinus*, *Microtus longicaudus mordax*, *Tamias minimus operarius*, and *Sorex vagrans monticola*. *Citellus variegatus grammurus* was seen. A beaver, *Castor canadensis frondator*, was obtained from a short distance down the valley, and a lodge and dam were observed nearby.

The authors wish to express their appreciation to Dr. Hartley H. T. Jackson, who verified the identification of the specimen.—William J. Koster and Ronald R. Clothier, *University of New Mexico, Albuquerque, New Mexico.* *Received June 4, 1951.*

ARIZONA SPECIMENS OF THE BLACK-FOOTED FERRET

Inasmuch as the most westerly part of the known range of the rare black-footed ferret (*Mustela nigripes*) is in Arizona, in the country north of Williams to the southern rim of the Grand Canyon, it would appear of value to record the two Arizona specimens known to us.

A black-footed ferret, now in the Biological Surveys Collection, was taken at Springerville, Apache County, in extreme east-central Arizona, on January 19, 1917. On August 26, 1929, Preston Mercer, then a Biological Survey employee, collected a ferret in the Red Lake farming district north of Williams in Coconino County. The skull of this animal was sent to the Biological Surveys Collection while the mounted body was for years on display at the Fish and Wildlife Service headquarters at Phoenix, Arizona. Recently this mounted body, which is pictured in the October, 1950, number of *Arizona Wildlife and Sportsman*, was sent to Washington D.C. and added to the Biological Surveys Collection.—Stanley P. Young and Arthur F. Halloran, *U.S. Fish and Wildlife Service, Washington, D.C., and Yuma, Arizona.* *Received May 3, 1951.*

THE LEAST WEASEL (*MUSTELA RIXOSA*) IN PENNSYLVANIA

Sutton (Jour. Mamm., 10:252–54, 1929) reported on the least weasel (*Mustela rixosa allegheniensis*) in Pennsylvania and based his distribution map upon skins received for bounty by the Pennsylvania Game Commission. The data he used covered the period 1925 to 1929. In 1948, we undertook to repeat this study to learn whether there had been any change in the range of this weasel in the twenty-five-year interim. This report is based upon the examination of 315 skins of the least weasel that were submitted for bounty in the three-year period February 1948 to February 1951. Most of these weasels were taken in 1948 and 1949. From March 1950 to February 1951, only 17 least weasels were probated. The drop in 1950 was associated with a general drop in the number of all weasels.

The 315 skins examined were from 187 townships in 31 counties. The distribution of these is shown in Figure 1. Each dot on the map represents a township where one or more least weasels have been taken. The two triangles (in Tioga and Mifflin counties) represent the most eastern localities of previously published records. Although the additional records of the last three years have filled in some of the gaps in the range, as published by Sutton, it is interesting that the range of *M. rixosa* in Pennsylvania is essentially unchanged from what it was twenty-five years ago.

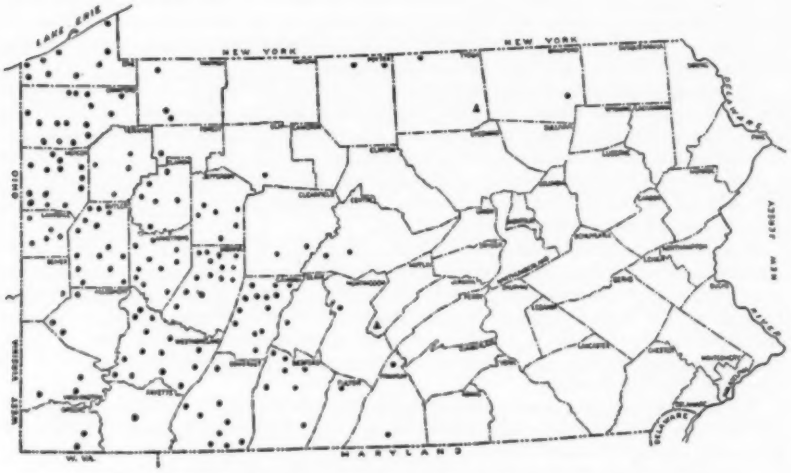

FIG. 1.—Distribution of *Mustela rixosa allegheniensis* in Pennsylvania

TABLE 1.—*Weasels taken in eight counties in Pennsylvania*

COUNTY	ALL WEASELS*	RIXOSA*	RIXOSA PER 1000
Butler	996	23	23
Cambria	1300	16	12
Crawford	1125	17	15
Erie	886	17	19
Indiana	1091	15	14
Mercer	709	18	25
Somerset	1862	19	10
Westmoreland	1515	18	12

* June, 1948–May, 1950.

Some idea of the relative abundance of the least weasel in western Pennsylvania may be obtained by comparing the number of least weasels killed with the total weasels killed during the same period. For this comparison the two fiscal years, June 1948 through May 1950, were used. In eight western counties, least weasels were taken at the rate of 10 to 25 per 1000 of all weasels taken. The average rate for the eight counties is 16 least weasels per 1000 weasels (Table 1).

It is not possible to compare the relative numbers of least weasels today with what they were in 1925–1929, as the 87 specimens reported by Sutton did not represent the total receipts of this species, but instead, were selected to show the greatest range. Actually, least

weasels were probably more numerous then than they are now, as weasels of all species in Pennsylvania were more numerous then.

Of the 315 skins examined by us, 19 were in white pelage, four were changing from white to brown, and one was changing from brown to white. The only one that was changing from brown to white was killed on December 17, 1949. It still had brown guard hairs and partly brown fur, but new white fur could be seen under the brown fur. Of the five that were changing from white to brown, one was killed February 6, the others were killed in the first week of March. Entirely white skins were observed during every month from November 20 to April 1. Although 61 per cent of the weasels examined were taken during November, December, and January, most of them were brown, only 8 per cent of those examined were white, or changing.—NEIL D. RICHMOND AND ROBERT D. MCDOWELL, *Pennsylvania Game Commission. Received June 16, 1951.*

LONG-TAILED WEASEL NEAR QUEBEC CITY

On November 19, 1950, Dr. D. A. Déry trapped a long-tailed weasel at Petit-Pré, Montmorency County, P.Q., about thirty miles north of Quebec City, which subsequently proved to be *Mustela frenata noveborecensis* (Emmons). This appears to constitute the first definite record for the occurrence of the long-tailed weasel north of the St. Lawrence River. Anderson (Catalogue of Canadian Recent Mammals, 1946, p. 66) restricts the northern limit of the range for this species to the "Eastern Townships" of Quebec and the southern counties of the province north of the Ottawa River. The latter is based on a male specimen taken at Grand Lake, Gatineau County, on October 28, 1943.

The Montmorency County specimen, a male, measures: total length, 425 mm.; tail (to tip of longest hair), 162 mm.; tail vertebrae, 127 mm.; hind foot, 46 mm. The skull has an occipito-nasal length of 43.5 mm. and the zygomatic breadth is 26 mm. Approximately two-fifths of the tail is black. The skin is now in the National Museum of Canada collection.—AUSTIN W. CAMERON, *National Museum of Canada, Ottawa, Canada. Received April 30, 1951.*

THE GRAY FOX IN ALBERTA

On January 12, 1950, a gray fox was trapped at Old Fort Point on Lake Athabaska (lat. 58° 36′ N., long. 110° 27′ W.) by Mrs. L. Peche of Fort Chipewyan, Alberta. The pelt was sent to the Alberta Game Branch where it was examined and then returned to the collector together with a statement indicating that it was a cross fox of no commerical value. Subsequently the pelt and skull of this specimen were acquired by the University of Alberta through the courtesy of Forest Ranger J. Sutter of Fort Chipewyan. To Mr. Sutter goes the credit for recognizing the unusual nature of the animal and for seeking further information concerning its identity. Dr. R. L. Peterson and Mr. S. C. Downing of the Royal Ontario Museum of Zoology have examined the pelt and skull and indicate that they are referable to *Urocyon cinereoargenteus ocythous.*

Mr. Sutter states that the gray fox has not been seen by residents of the Fort Chipewyan vicinity on any previous occasion. Information from government officials and fur dealers in Edmonton reveals that no other gray fox pelt has ever appeared in the fur catch of northern Alberta. This record extends the range of *Urocyon c. ocythous* some 800 miles to the northwest of Minot, North Dakota, which appears to be the nearest point at which this subspecies has been taken (Shantz, Jour. Mamm., 31:197–198, 1950).—J. E. MOORE, *Department of Zoology, University of Alberta, Edmonton, Alberta. Received May 7, 1951.*

AN OCCURRENCE OF THE RICE RAT (*ORYZOMYS*) IN WEST VIRGINIA

In May, 1951, the writers visited Mr. Jack Leppla and Mr. Albert Bauer at the Speidel Farm site (460H7), 2 miles NNE of Oglebay Park, Ohio County, West Virginia. This archeological site is located upon the divide separating Long Run and Short Creek, 2¾ miles east of the Ohio River, at an elevation of 1240 feet.

At a depth of eleven inches (plow depth nine inches), at the base of what appeared to be

an undisturbed occupation level, a number of bones and Indian artifacts were unearthed by Mr. Leppla. Most of the bones were cracked or burned, or showed signs of having been worked by the Indians. Species identified were elk (*Cervus canadensis*), deer (*Odocoileus virginianus*), bobcat (*Lynx* sp. ?), woodchuck (*Marmota monax*), chipmunk (*Tamias striatus*), squirrel (*Sciurus* sp.?) and turkey (*Meleagris* sp.?).

At the same level, Mr. Leppla uncovered the remains of three rice rats (*Oryzomys palustris* sp. ?): one adult, represented by the anterior half of a skull; two mandibles and skeletal parts; and two juveniles, represented by one mandible and skeletal parts. These were all found in close association. The bones showed no evidence of having been used by man. They were complete and unburned. It would appear that the occurrence of the animals was independent of the Indian occupation, but probably at no earlier date than the occupation itself. This appears to be the first known occurrence of the rice rat in West Virginia.

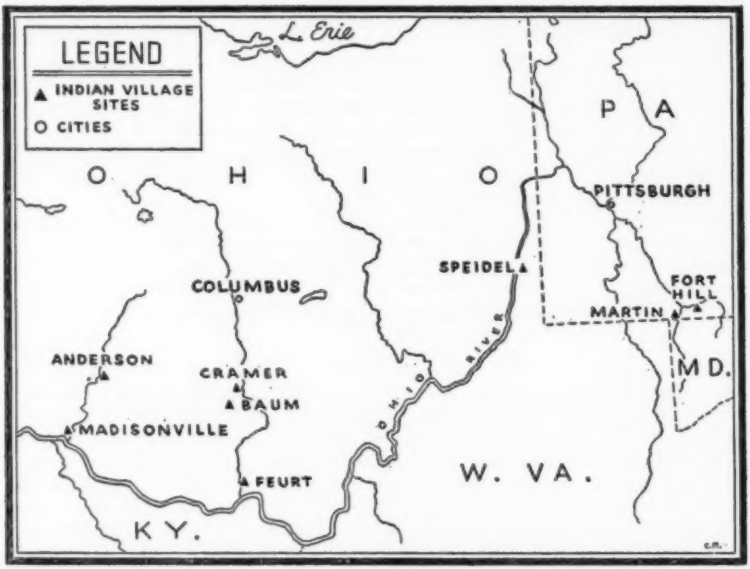

FIG. 1.—Distribution of rice rat remains from archeological sites in the upper Ohio Drainage.

Preliminary examination of the artifacts excavated at 460 H7 indicates that this site was occupied primarily by Indians of the Late Prehistoric period, 1200 A.D.–1600 A.D.

The cultural materials are closely related to those of the Fort Ancient culture of southern Ohio. The other occurrences of the rice rat from the upper Ohio drainage (Fig. 1) have been at prehistoric Indian sites of this same general period. Mills (Ohio Arch. and Hist. Quart., 15:45–136, 1906) has reported them from the Baum site near Chillicothe, Ohio. Goslin (Ohio Indian Relic Collector's Soc., Bull. 26: 19–22, 1951) records the appearance of the rice rat in Ohio at the Madisonville site near Cincinnati, the Anderson site near Lebanon, the Feurt site near Portsmouth, and the Cramer site near Chillicothe. These are all Fort Ancient sites. Gilmore (Jour. Mamm., 27:227–34, 1946) refers to two excavations in southwestern Pennsylvania, which Cresson has reported in an unpublished manuscript. At both the Martin site in Fayette County, Pennsylvania, and the Fort Hill site in Somerset County, Pennsylvania, rice rat skeletal remains were found, apparently in temporal association with

the Late Prehistoric Indian occupation. The occurrence of the rice rat in southwestern Pennsylvania, southern Ohio, and northern West Virginia, all associated with Indian villages along the upper Ohio drainage which are roughly contemporaneous, appears to indicate an extensive reduction in range from at least 1600 A.D. until the present time. One questionable specimen of recent origin was recorded for the Madisonville area by Langdon (Jour. Cincinnati Nat. Hist. Soc., vol. 3, No. 4, 1881). No living specimens of the rice rat have been taken within the area to date.

This reduction in range coupled with the rather aberrant appearance of the adult skull now in the Section of Mammals, Carnegie Museum (broad rostrum and exceptionally large cheek teeth), suggests the desirability of assembling skeletal remains from the various excavations for comparative study.—JOHN E. GUILDAY AND WILLIAM J. MAYER-OAKES, *Carnegie Museum, Pittsburgh 13, Pa. Received July 12, 1951.*

CUVIER'S BEAKED WHALE FROM HAWAII

In a Honolulu newspaper, dated January 28, 1950, report was made, and a photograph printed, of a small whale, identified as a False Killer Whale, *Pseudorca crassidens*, washed ashore, January 25, at Kalae, South Point, Kau District, Hawaii, Hawaiian Islands.

While making a series of field trips on the Island of Hawaii in October, 1950, the writer and two friends, Mr. and Mrs. Paul L. Breese, of Honolulu, heard of, and decided to investigate, a second report of another, or the same (we didn't know which), dead whale beached at Kalae. Therefore, on October 25, the three of us drove to Kalae and located a 20-foot whale skeleton on the beach.

The battered skull of this whale was obtained and sent to the Museum of Vertebrate Zoology, University of California, Berkeley, and was subsequently identified by Dr. Seth B. Benson as that of a Cuvier's Beaked Whale, *Ziphius cavirostris* Cuvier.

Realizing that some confusion existed concerning either the number of whales washed ashore at Kalae or the identification of the one reported in January, I attempted to locate photographs of the animal, or animals. Through the efforts of Miss Joan Demond and Mr. and Mrs. R. J. H. Farrar, of Honolulu, excellent data and photographs, taken by Mr. Albert G. Alba, of Naalehu, Hawaii, of the animal washed ashore, January 25, 1950, were obtained. These data and photographs proved that this animal was not a False Killer Whale, but a male Killer Whale, *Grampus rectipinna*.

Then, washed ashore at Kalae, between January 25 and October 25, 1950, were two whales, a male Killer Whale and a Cuvier's Beaked Whale. The latter, a cosmopolitan ziphiid, has, as far as is known, never been previously reported from the Hawaiian Islands.—LAWRENCE P. RICHARDS, *Museum of Vertebrate Zoology, University of California, Berkeley, California. Received May 1, 1951.*

THE STATUS OF THE BAT GENUS *REITHRONYCTERIS*

In 1898 (Proc. Acad. Nat. Sci. Philadelphia, 50: 333–37), Gerrit Miller described a new genus of Phyllonycterinae from Jamaica which he named *Reithronycteris*. This he compared with *Phyllonycteris*, known by two species, both from Cuba. Unfortunately he had only the referred species, *P. sezekorni*, not the type species, *P. poeyi*. In 1906 (Proc. Biol. Soc. Washington, 19: 84), having seen *P. poeyi*, he realized that *P. sezekorni* was generically distinct and separated it, together with some later described species, as the genus *Erophylla*. Most of the characters used to distinguish *Reithronycteris* were then found merely to distinguish this Jamaican form from *Erophylla*. In 1907 (U. S. Nat. Mus. Bull., 57: 174–75), Miller redefined *Reithronycteris*, distinguishing it from the now monotypic *Phyllonycteris*, and correcting certain errors in the original description. Only one character was now found to distinguish *R. aphylla* generically from *P. poeyi*, the presence of a trough on the ventral surface of the brain case. Since Miller's (*loc. cit.*, 1907) discussion, two additional species of *Phyllonycteris* have been described, *P. major* (Anthony, Bull. Amer. Mus. Nat. Hist., 37: 567–68, 1917) of Puerto Rico (from fairly ancient cave deposits) and *P. obtusa* (Miller, Smithsonian Miscl. Coll., 81: 11–12, 1929) of Hispaniola (from owl-pellet material).

Miller erected the genus *Reithronycteris* on the basis of a single alcoholic specimen (including the removed skull) without definite locality or other data. Beyond the fact that the specimen came from Jamaica, and was collected sometime before 1898, nothing is known about it. Until recently, no additional material had come to light, to the knowledge of the writer. The Jamaica Institute has now no specimens, although the type of *Reithronycteris* was originally there.

In 1951 (Amer. Mus. Novitates, 1519: 1–29), Koopman and Williams, in discussing the fossil bats collected by H. E. Anthony in Jamaica, referred some cave material to *Reithronycteris aphylla*. Since, however, the material was fragmentary, edentulous, and lacked the diagnostic basicranial region, it was impossible to be altogether sure that *Reithronycteris* rather than *Phyllonycteris* was the form represented. Hence, Miller's specimen remained the only material on which the genus *Reithronycteris* could be based.

In the summer of 1950, the author, together with Ernest E. Williams, Max K. Hecht, and Bessie M. Hecht, spent six weeks in Jamaica collecting living and fossil amphibians, reptiles, and mammals. In the course of investigating several promising-looking caves, for fossils, a good Recent surface deposit was discovered which yielded a large quantity of land vertebrate bones. This deposit was located on the property of Mr. Jack Lewis, at Antrim, near the village of Runaway Bay, St. Ann's parish. It was located on a small ledge about ten feet above the ground. The cliff above it was somewhat overhanging so that the back of the ledge could be said to form the floor of a tiny cave. This deposit, apparently left by owls, consisted of only a superficial covering at the front of the ledge where it was exposed to rainfall, but reached a depth of approximately six inches at the back where it was protected by the overhang. There was tendency for the bones to be cemented together by organic material although the original owl pellets had almost completely disintegrated.

A large quantity of material has been removed from this deposit and much time has and must still be spent sorting and identifying the great mass of bones. When this is completed, the resultant material will be the subject of a separate later paper. Some preliminary statements about the mammalian genera represented may, however, be made at this time. Besides the introduced *Rattus* and *Mus* which unfortunately make up the great bulk of the mammalian bones, five genera of bats are represented.

The exact age of the deposit is rather uncertain. Since *Rattus* bones predominate in even the oldest part of the deposit, it is evident that 450 years would be the maximum age for any part of it. Some of the bones have a very fresh appearance and are perhaps not older than a few decades. It seems probable, therefore, that the bulk of the deposit is between 50 and 400 years old.

Most of the bat material pertains to the stenodermine genera *Artibeus* and *Ariteus*, but one complete and one fragmentary lower jaw of the glossophagine genus *Monophyllus*, and a mandible of *Erophylla* have also been recovered to date. Of the fifth genus, one complete skull, a partial skull, some skull fragments, and a number of mandibles have so far been recovered. Examination of the complete skull, which, however, lacks all but one molar tooth, leaves no doubt but that the species is *Reithronycteris aphylla*, since the diagnostic trough in the base of the brain case is well preserved. This second complete skull of the genus is now MCZ #45140, while the other material is in the American Museum of Natural History.

In connection with this new material and in view of the changed conception of the genus *Phyllonycteris* which has emerged, it was felt that a re-evaluation of the status of *Reithronycteris* was in order. First an attempt has been made to find external characters differentiating the two genera. Unfortunately, of the three species of *Phyllonycteris*, *obtusa* and *major* are known only from skeletal remains. Hence the comparison could be made only between the type alcoholic of *Reithronycteris*, now in the United States National Museum, and alcoholics of *Phyllonycteris poeyi* in the same museum. Aside from certain size and color differences, no external characters can be found to differentiate the two forms, and these can hardly be considered to be of generic value.

A thorough comparison has been made of the skull of *Reithronycteris* with those of the

three species of *Phyllonycteris*. No constant characters were found to distinguish the two genera other than those involving the basicranial region and molar form. There seems to be no approach to the *Reithronycteris* condition in the basicranial region of any *Phyllonycteris*, but in molar shape the differences appear to be quite slight. In *Phyllonycteris poeyi* the upper molars, particularly M^2, have a somewhat quadrate form, whereas in *Reithronycteris aphylla* the labial side is somewhat lengthened giving each molar a more triangular form. This difference is clearly shown in Miller's figures (Miller, *loc. cit.*, 1907). *P. obtusa*, however, shows a somewhat intermediate condition, although closer to *P. poeyi*. This tooth character, therefore, seems to be of no more than specific value. Miller mentions other tooth characters, but these appear to be too greatly subject to individual variation to have much value even on a specific level.

One factor which enters the problem is the rather high degree of individual variation in skull and tooth form which occurs in *Phyllonycteris*. Some of this variation is apparently sexual since males of *P. poeyi* tend to have heavier, more robust skulls than do females. The type of *Reithronycteris* is a male and appears to have been a particularly robust individual of its species, as compared with the Antrim and fossil skulls, most of which may have been females. It is possible that sexual dimorphism has been more pronounced in *Reithronycteris* than in *Phyllonycteris*.

In any case, the genus *Reithronycteris* appears to stand or fall on the character of the basicranial trough. This is a most unusual structure. To the knowledge of the writer nothing like it is known in any other mammal. In life it must have occupied a site dorsal to the nasal passage just anterior to its junction with the pharynx, since it lies entirely behind the false palate.

Mr. Samuel B. Macdowell of Columbia University has very kindly studied the complete Antrim skull of *Reithronycteris* in comparison with a skull of *Phylloncyteris poeyi*. He believes that the trough in question may have enclosed a dorsal diverticulum of the nasopharynx. Since, on the basis of tooth pattern together with rather meager direct evidence, the Phyllonycterinae appear to be nectar-sucking forms, and as *Reithronycteris* is the most specialized of its subfamily, Mr. Macdowell suggests that such a naso-pharyngeal diverticulum might operate as a vacuum device to produce suction, which could have considerable advantage in extracting the nectar from long tubular flowers. *Reithronycteris* may thus represent the culmination of phyllonycterine specializations for nectar feeding. This, however, is hypothetical and will remain so unless and until a fresh or alcoholic specimen can be dissected before the skull is cleaned. Unfortunately, since the species may already be extinct (Allen, Extinct and vanishing mammals of the Western Hemisphere, 1942), there seems little probability of this.

There can be no doubt that *Reithronycteris* is closely allied to *Phyllonycteris*, considerably more so than either is to *Erophylla*. It represents *Phyllonycteris* on Jamaica just as the species of *Phyllonycteris* represent one another on the other Greater Antillean islands. *Reithronycteris* appears to be closest to *P. obtusa* and may be looked upon as a specialized derivative of that form. As an expression of this relationship we might consider *R. aphylla* to form a superspecies with the species of *Phyllonycteris*; *Reithronycteris* then being sunk as a synonym.

On the other hand, there is the highly peculiar trough in the basicranial region with its implications of additional specializations for nectar sucking. This specialization, which sets *Reithronycteris* off from both *Phyllonycteris* and *Erophylla*, would find its expression in retaining *Reithronycteris* as a separate genus.

Since we cannot express both the close relationship and the greater degree of specialization by any one procedure, a compromise would appear to be the only recourse. *Reithronycteris* is, therefore, reduced to a subgenus and the Jamaican form will then stand as: *Phyllonycteris* (*Reithronycteris*) *aphylla* Miller.

The writer wishes to express his appreciation for the gracious hospitality extended him by Mr. Jack Lewis, whose aid in locating the Antrim deposit was indispensable. Acknowledgments are also due to Dr. C. Bernard Lewis of the Jamaica Institute, Dr. David H. John-

son of the Division of Mammals, United States National Museum, and to the Mammal Department of the American Museum of Natural History for making available the collections in their care. It is also a pleasure to acknowledge the aid generously given by Mr. Samuel B. Macdowell of Columbia in the interpretation of the skull of *Reithronycteris*.—KARL F. KOOPMAN, *511 W. 113 St., New York 25, N.Y.* *Received April 27, 1951*

NOTES ON THE DENTITION OF THE GOLDEN MONKEY, *RHINOPITHECUS*

While working in the United States National Museum on Recent monkeys from China, I came across a series of skins and skeletons belonging to the golden monkey, *Rhinopithecus roxellanae* A. Milne-Edwards, from the province of Szechwan, southwest China. This material was collected in 1924 and 1938 by Dr. D. C. Graham of Chengtu, Szechwan, and the 1938 material was entered in the catalogue of the Mammal Department of the Museum in the same year in which the first part of Dr. Allen's great work on The Mammals of China and Mongolia (Amer. Mus. Nat. Hist., 1938) was published. Consequently, this *Rhinopithecus* material of the Washington Museum has not been recorded by Allen, and since his work for many years will remain the standard reference work on the Recent mammals of this area it seems worthwhile to put Dr. Graham's material on record. The series consists of the following specimens:

Two juveniles, flat skins and skeletons; male (USNM no.268896) with M_2 erupting, milk dentition except for id_1, and a female (USNM no. 268889) with M_2 not yet erupted, full milk dentition. Wen Chuan Hsien, Szechwan, China, March, 1938.

One subadult, stuffed skin with skull and leg bones, male (USNM no.258986), M_2 not yet erupted, permanent incisors erupted and unworn, milk canines and molars still present. Wen Chuan Hsien, Szechwan, China, February, 1938.

Two adult males: USNM no. 240920, flat skin without skull, Suifu (?), Szechwan, China, 1924, and USNM no. 268887, flat skin and skeleton, skull slightly crushed above, Wen Chuan Hsein, Szechwan, China, March 1938.

Nine adult females, all from Wen Chuan Hsien, Szechwan, China: USNM no. 268886, flat skin and skeleton, P^3 on both sides congenitally absent, a fourth molar in left upper jaw, October, 1938; USNM no. 268888, flat skin and skeleton, March, 1938; USNM no. 268890, flat skin and skeleton, left P_4 absent, but condition of bone shows that this element had been present, alveolus almost, but not completely, closed, March, 1938; USNM no. 268891, skeleton without leg bones, March, 1938; USNM no. 268892, skeleton without leg bones, left I_1 rotated, March, 1938; USNM no. 268893, skeleton without leg bones, lower left C rotated, March, 1938; USNM no. 268894, flat skin and skeleton, P^3 on both sides congenitally absent, P^4 rotated on both sides, occlusion normal otherwise, March, 1938; USNM no. 268895, flat skin and skeleton, March, 1938; USNM no. 268897, flat skin and skeleton minus two of the leg bones, March, 1938.

It will be noticed that in this comparatively small series of skulls there are two instances of congenitally absent upper third premolars, as well as a case of a fourth molar in the upper jaw.

As far as my experience with the Recent Asiatic monkeys goes, especially of the genera *Presbytis*, *Trachypithecus*, *Nasalis*, *Macaca*, and *Cynopithecus*, of which more than seven hundred skulls have been available to me in the Dutch natural history museums as well as in those in New York, Baltimore (Dr. Adolph H. Schultz's personal collection), and Washington, D.C., it is very exceptional for an Asiatic cercopithecoid monkey to lack the front upper premolar, while the occurrence of a fourth upper molar is even more remarkable. In the five monkey genera mentioned above I cannot recall to have seen more than one or two instances of missing P^3s, while an M^4 has never been observed by me to occur in any of the adult skulls of these genera. As a matter of fact it is Colyer (Variations and diseases of the teeth of animals. London, 1936, p. 26) who states that he found no numerical variations in seventeen specimens of *Rhinopithecus* examined by him, while in *Presbytis*, *Trachypithecus*, and *Macaca* mention is being made of one case of absence of the maxillary left second premolar in *Presbytis aygula hosei* (Thomas) (*op. cit.*, p. 37), and of two cases of occurrence of

fourth upper and lower molars in *Macaca* (in a total of 901 skulls examined; *op. cit.*, pp. 26 and 49). In a series of 289 *Semnopithecus* skulls Colyer (*op. cit.*, p. 35) found again but one instance of the presence of fourth molars. No discussion is included here on the occurrence of extra cusps and the like, which, as it seems, are actually nothing but stages in the development of extra teeth, but cannot be considered as numerical variations of the teeth, which concern us in the present paper.

Rhinopithecus as well as the other monkey genera show different evolutionary stages of development of the dentition along lines which seem to be pretty much the same in all of these forms. There is an evident tendency toward reduction of the number of the dental elements, just as is the case in man, a tendency that becomes apparent when subfossil and fossil remains of the skull and mandible belonging to these very genera are taken into account. Pleistocene and prehistoric material of the genus *Macaca* from China and from Celebes has shown that the maxillary as well as the mandibular third molars are on their way toward elimination, a condition shown by the relatively larger size which this molar has in the early species as compared with those now living, and the occasional absence of it in the Recent forms. There is also an evident trend toward reduction of the maxillary third (anterior) premolar, but much more material than is at present available would be needed to settle these things definitely.

It is, therefore, not so peculiar for a Recent *Rhinopithecus* to lack completely the P^3, and, in my opinion, this is only the more to be expected since in *Rhinopithecus*, unlike the other Asiatic cercopithecoid genera mentioned above, the P^3 as a rule is already definitely smaller than the P^4. In *Presbytis*, *Trachypithecus*, *Nasalis*, *Macaca*, and *Cynopithecus*, P^3 never is so small in comparison with P^4, and *Rhinopithecus* would seem, therefore, to represent a more advanced evolutionary stage as far as this trend goes.

It is different, however, for the occurrence of fourth molars. One would hardly expect to find an M^4 in a ratio of one out of ten adult skulls, actually a percentage of 10 ± 9.4, in a monkey that is so clearly more advanced in the process of reducing the number of its teeth than, say, *Macaca* or *Semnopithecus*, in which the percentages of occurrence of fourth molars are 0.22 ± 0.16 and 0.34 ± 0.11, respectively. In *Pongo pygmaeus* (Hoppius), the orang-utan well known for its high incidence of fourth molars, the occurrence of fourth molars is twenty per cent. This is Selenka's (Menschenaffen (Anthropomorphae). Studien über Entwicklung und Schädelbau. I. Rassen, Schädel und Bezahnung des Orangutan. Wiesbaden, 1898) figure so often mentioned in the literature although it is actually lower, 12 ± 1.5 per cent, if subsequent collections reported upon by Hrdlička (Proc. U. S. Nat. Mus., 31:539–68, 1907), Colyer (*loc. cit.*), and Hooijer (Zool. Med. Mus., Leiden, 29:175–301, 1948) are taken into account.

Thus, the occurrence of an M^4 in *Rhinopithecus* seems to be a major variation in the dentition that is worth recording, although about the significance of this occurrence we are somewhat left in the dark. It has been stated by some authors that M4s in placental mammals point to earlier stages in mammal evolution nowadays represented by the marsupials, while it has also been stated that, particularly in the case of the orang-utan, the occurrence of M4s must be looked upon as evidence of the tendency toward enlargement of the masticatory surface of the teeth, a sort of need for additional chewing space that would already have thrown the surface of the cheek teeth of the orang-utan into the numerous fine wrinkles which now characterize these teeth. Unfortunately the studies of the prehistoric and Pleistocene orang-utan teeth from Sumatra, Java, and south China (Hooijer, *loc. cit.*) have not led to the establishment of the fact whether these early races of *Pongo pygmaeus* (Hoppius) actually more often possess fourth molars than the Recent Sumatran and Bornean race do. The wrinkle system on the molars is not inferior in complexity to that on the Recent ones. The only point that could be brought out with regard to the problem of the fourth molar was that the percentage of occurrence of M4s probably was much the same as that in the Recent orang-utan.

In this connexion it may be mentioned that Eugène Dubois, while finding, with the famous skull cap, two molars at Trinil in Java, and attributing these remains all to one and

the same individual which he named *Pithecanthropus erectus*, he actually found a left M^3 and a right M^4 of the orang-utan (Hooijer, *op. cit.*, pp. 272–80). If these two molars did belong to one and the same individual, Dubois would have made a find that according to the calculus of recent probabilities is made only in 1.3 ± 0.5 per cent, or one time out of fifty or a hundred. It seems very probable that the incidence of fourth molars in the orang-utan was higher in former times than it is in the Recent orang-utan, but nothing can be proven about this as long as so little is known about it in the history of the dentition of this ape. The subfossil Sumatran orang-utan differs from the living in the relative size of the teeth, and is, on the average, sixteen per cent larger than the living form, and the various evolutionary trends of development in the dentition observed are identical with those found upon comparison of the cave Moor macaque of southwest Celbes with the living Celebean macaque (Hooijer, Verh. Kon. Ned. Akad. v. Wetenschappen Amsterdam, afd. Natuurk., sectie 2, vol. 46, no. 2, 1950).

Thus far we know very little about the history of *Rhinopithecus*. Some material of a subadult skull and mandible fragments are present in the Pleistocene collection from Yenchingkou, near Wanhsien, in Szechwan, beyond the actual distribution of *Rhinopithecus* as shown by Allen (*op. cit.*, p. 299). This material, which is being kept in the American Museum in New York, is only suggestive of *Rhinopithecus roxellanae* A. Milne-Edwards, having been somewhat larger in the Pleistocene than it is now.

A brief description of the fourth molar found in skull no. 268886 of the United States National Museum collection may follow. The upper left fourth molar is two-rooted, and the crown is oval in outline and elongated antero-posteriorly. It bears a distinct central cone surrounded by a well-developed, crenated cingulum that rises into a point anteriorly, and forms a sizable point at the posterior end. When seen from the inner or outer side the tooth looks somewhat like a pinniped tooth, or like one of the extinct triconodonts. The dimensions are: anteroposteriorly, 9.8 mm.; transverse, 6.2 mm.; height of cingulum from base of crown, 3–4 mm.; height of central cusp from the same, 5.6 mm.; length of anterior root, 11 mm.; of posterior, almost the same. The posterior root is curved forward at the apex.—D. A. Hooijer, *Rijksmuseum van Natuurlijke Historie, Leiden, Netherlands. Received November 24, 1950.*

APODEMUS FLAVICOLLIS ALPICOLA, N.N.

For *Apodemus flavicollis alpinus* Heinr., Zool. Jahrb., LXXX, 1/2, p. 114, 1951, preoccupied, I propose *Apodemus flavicollis alpicola* n. n. The name "*alpinus*" is already preoccupied by *Mus sylvaticus alpinus* Burg, 1921, the latter being regarded to be a synonym of *Apodemus sylvaticus sylvaticus* L.—Gerd H. Heinrich, *Dryden, Maine.*

CORRECTION

In my recent note in this Journal, Vol. 32, No. 4, on "Peak Populations of *Peromyscus maniculatus gracilis* in Northern Ontario" I erroneously referred to the subspecies *gracilis*. This subspecies possibly does not extend much further north than the Chapleau area.—A. de Vos, *Division of Fish and Wildlife. Maple, Ontario.*

REVIEWS

Gregory, William King. EVOLUTION EMERGING. The Macmillan Company, New York. Vol. I, pp. 1–736, text; vol. II, pp. 1–1013, illustrations; 1951. Cloth bound. Price $20.00.

Evolution Emerging includes essentially the materials that were covered in the author's courses at Columbia University. It is basically a discussion of the origin and evolution of the different groups of the animal kingdom with particular emphasis on the vertebrates. The author has emphasized the critical stages in evolution involving the transitions between some of the higher taxonomic groups. Most of his ideas are based on sound paleontologic evidence like the fossil materials in the transition from fish to amphibians and from reptiles to mammals. Some of the other transitions are not so completely demonstrated in our fossil record, but he rather clearly shows that there can be little doubt concerning the evolutionary changes involved. He has drawn widely from sources other than his own research for the information published in these volumes. This, then, should not be looked upon in every instance as the original source of the materials and of the ideas presented, though many of them were original with the author.

The author adopts a broad concept of evolution. He feels that evolution is the history of energy systems and of all their deviates. It deals with the processes and results of the transformation of energy and matter viewed against the background of time and space. He makes no special effort to prove evolution, which he adopts as a postulate, but discloses facts concerning it.

Certain theories on the origin of the earth are briefed, particularly the planetesimal hypothesis and also more recent variates of the theory. He attempts to prepare the reader to think in terms of geologic time.

Since 1914 the author has stressed the importance of a correct interpretation of habitus and heritage in any understanding of organic evolution. It might be considered as the theme in this compendium of his life work and in the research of others that he has adopted. Habitus is the general form and appearance of an animal in its relation to the environment, i.e. "the fish-like habitus of ichthyosaurs and whales." Heritage is "the older or deeper seated characters that reveal the animal's true place among the classes and orders of the animal kingdom."

Sources of energy and emergence of living matter are discussed briefly. Primitive animals evolved from primitive plants. It is assumed that the first animals may have been motile forms much like the rhizopod protozoan *Dimorpha mutans*. The evidence of Pre-Cambrian life is reviewed with emphasis on the conclusions of Percy E. Raymond. The author evidently accepts graptolites as a distinct class of coelenterates, and does not mention the possibility of their being related to primitive chordates. He thinks trilobites are derived from a common Pre-Cambrian stock with all arthropods, and he seems to agree with Stromer that these in turn were derived from primitive annelids. The different phyla of invertebrates are reviewed and suggestions are made on their origin and phyletic relationships. The gastropods are well illustrated.

Seven theories on the origin of the vertebrates from lower forms are reviewed, then the author gives his *eclectic theory*, which proposes that—"the vertebrates belong to an 'enterocoelic' superphylum which was entirely different from the 'teloblastic' series named Trochozoa, which includes the annelids and arthropods." The prochordates were predaceous forms derived from food-sifting forms. "The balanoglossids in their adult forms seem to lead away from the direction of the vertebrates and so do the ascidians." Amphioxus is a true basic chordate though it is specialized in certain features and perhaps degenerate in others.

The author's studies on the fish is one of his greatest contributions to our knowledge of the animal kingdom. This is well reviewed and adequately illustrated in these volumes. This is particularly true of the Teleosts. His review of the amphibians, birds, and reptiles covers all of the critical steps, and here again are illustrations of interest to anyone who might be concerned with the study of vertebrates. Some of his most outstanding contributions are

his studies on the mammal-like reptiles. In the mammals he has been particularly concerned with the primates and their relationships to the Hominidae. Unfortunately, due to the nature of the evidence from the fossil record, this is based primarily on the teeth. His adaptive radiation charts of the marsupials, viverrids, and mustelids, to point out examples, are stimulative, but the reader must not confuse these with true phylogenies with which they sometimes agree rather closely. Some of the illustrations, especially in the mammals, seem to have been done hastily, but most of them are excellent. There is no table of explanation for the abbreviations on the figures, though most of these will be understood. The illustrations are in pen-and-ink line drawings. The text is quite abbreviate.

Perhaps the author's most venturesome idea is his attempt to explain the origin of the monotremes from the phalangerid marsupials by his palimpsest theory. This he explains by his interpretation of habitus and heritage features. He thinks that many characters in monotremes are merely convergent towards reptilian characters. The female reproductive system, he explains as an arrested development at a stage in which the right and left oviducts were still separate. Then there was a secondary increase in yolk with large eggs and an oviparous rather than ovo-viviparous habit. He would, therefore, include the monotremes and the marsupials in a new subclass Marsupionta.

These volumes are excellent reference books and should be available to everyone who is concerned with the study of vertebrates.—R. A. Stirton, *University of California.*

Simpson, George Gaylord. Horses. New York. Oxford University Press. xxiv + 247 pp. illustr. September 13, 1951. Price $6.50.

Doctor Simpson is well qualified for the task of following the "Story of the Horse Family" through sixty million years of history. He began his study of the group in 1924. The presentation of the subject has been no easy task. Doctor Simpson has brought together, from the far corners of the earth, facts regarding the horse. He has attempted to put this information together for the layman, nonscientific student, and teacher alike. The story of the horse is based upon facts, and not complicated by a great mass of details. This story furnishes the best examples of the evolution and of the development of breeds of horses thus far brought together. It was necessary, in attempting to present a clear and understandable picture of the vast subject in its simplicity for the layman, to include many explanations which will appear as unnecessary details to the advanced student. Unfortunately, the 32 plates with numerous figures are placed in the front of the book and not with the text where the figures would be most useful as well as helpful in holding the attention of the reader. The book is divided into two parts.

Part one: "Living horses," consists of 9 chapters. Doctor Simpson starts with the thought-provoking question, "What is a horse?" He tells of man's concept of the horse, and describes the wild members of the family. He begins the discussion of the development of breeds of horses with the earliest known stocks, followed by a discussion of European breeds in America, and the development of American breeds. The gaits of horses are discussed and figured by a block diagram which is very useful to the reader. Chapter 9 deals with color in horses. Many readers will skip most of this. Some will try raising rabbits to see how color is inherited. A sharp reader will come up with the answer that black haired parents can have redheaded children.

Part two: "The lineage of the Horse" follows the fragmentary genealogy of the horses, through the ages, from a time when our ancestors looked down upon them from lofty trees until later when they stalked them for food, prior to domestication. The genealogy or lineage of the horse family is based upon fossil evidences that have been accumulated during the past century and a half, and pieced together, in part, by the many students of horse history. Doctor Simpson has taken this vast array of facts and presented them in an interesting story of the development of the horse from "Eohippus" to *Equus*. He tells of the many side branches of the horse family and clearly shows that it has not made a straight line development through the sixty million years from little "Eohippus" to the modern horse. The development of the limbs, teeth, skull, and brain of the horse are followed through their various changes through time. The changes in teeth are shown, from the

low-crowned semi-omnivorous type to the high-crowned grazing type. The development of the limb is followed through its evolution from that of the four-toed scampering "Eohippus" to the present one-toed horse. Chapter 20 deals with a group of mammals that once lived in South America, not related to the horse though horse-like in appearance, and reached the one-toed stage of development ahead of the horse. Chapter 25 summarizes the "Patterns of Evolution" and chapter 26, the "Explanations of Evolution."

The book will be found very useful to the student of mammalogy and teachers of Historical Geology and Evolution.—CLAUDE W. HIBBARD, *Dept. of Geology, University of Michigan, Ann Arbor, Michigan.*

RECENT LITERATURE

(Conducted by G. S. Miller, Jr., Emma Charters, D. H. Johnson, and R. H. Manville)

[Reprints of this section may be purchased from the Corresponding Secretary]

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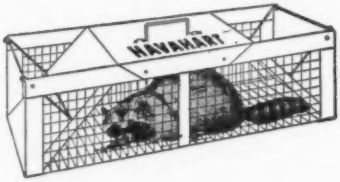
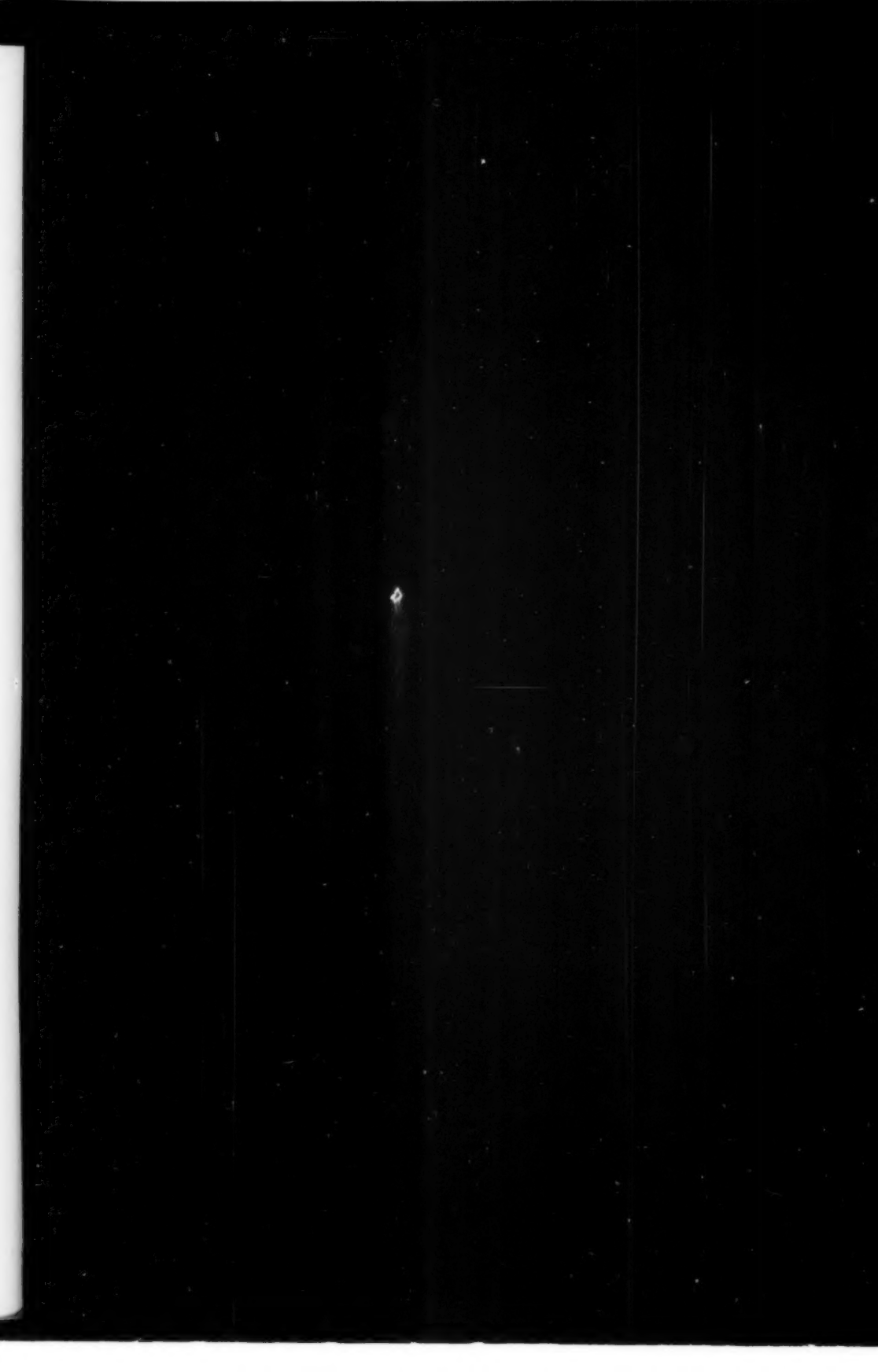
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